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EXPERIMENTAL STUDIES ON THE DURATION OF LIFE. XVI. LIFE TABLES FOR THE FLOUR BEETLE *TRIBOLIUM* *CONFUSUM* DUVAL¹

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I

UP to the present time (see Pearl and Miner, 1935 and 1936) there have been published complete or abridged life tables for representatives of three orders of insects, namely, the Orthoptera (*Blatta orientalis*), Lepidoptera (*Telea polyphemis* and *Acrobasis caryae*), and Diptera (*Drosophila melanogaster* and various of its mutants). To this meager list we are able now to add life tables for a fourth order, the Coleoptera, as represented by the tenebrionid beetle *Tribolium confusum* Duval. This form has been widely used in recent years in experimental population studies, to which it is particularly well suited. The known facts about the general biology of *Tribolium* have been summarized by Park (1934), and therefore need not be discussed in any detail here. Normally and usually it spends its entire life in flour or meal or processed cereals of various sorts. Its life cycle includes egg, larval, pupal and adult (imaginal) stages. The time duration of the pre-imaginal stages, taken together, varies greatly with the environmental conditions

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as to food, temperature, etc. Most of this variation is in the duration of the larval instar stages, the egg and pupal stages being more constant in duration. The following statement (Park, 1934, p. 43) gives the general picture under standard laboratory conditions: "in white patent flour at a temperature of 28° C., and a relative humidity of approximately 50 per cent., an entire life-cycle from egg to adult is completed in about 50 days."

Precise information as to the duration of adult (imaginal) life has been hitherto meager. Good (1936, p. 38) states that the adult life of *Tribolium* "is among the longest recorded for the stored-product insects." As examples of extreme longevity in *T. confusum* he cites (p. 39) the cases of 7 individuals that exhibited adult life durations ranging between 2 years, 347 days and 3 years, 271 days. From life history studies made upon 25 pairs of each of the two species *T. confusum* and *T. castaneum* Good (p. 39) found that average adult life of "*T. confusum* males is about 634 days, and of females, 447. For *T. castaneum* the average for males is 547 days, and for females, 226 days." It will be seen from Table 1 *infra* that the present larger samples for *Tribolium confusum* under different experimental conditions gave considerably lower averages than these.

In view of the manifest insufficiency of systematic information as to the order of dying of adult *Tribolium*; the important need, for population research and other experimental work on this form, to have at hand the results of a precise and comprehensive actuarial analysis of its life duration; the theoretical interest of such results from a comparative point of view (*cf.* Pearl and Miner, 1935); and the amenability of this beetle to the necessary type of experimentation; it was decided to put through a series of life table experiments with it.

II

Two series of experiments were performed. They were carried out in the period between December 23,

1935, and July 20, 1937. They included in total 800 beetles, divided as follows:

Series I. *Fresh-flour males*. 400 males. Flour renewed every 5 days.

Series II. *Fresh-flour females*. 400 females. Flour renewed every 5 days.

In both series the experimental unit was a half-pint milk bottle containing 32 grams of fresh "Ceresota" patent, unbleached flour and 16 *Tribolium confusum* individuals, all of the same sex and all from the same inbred stock culture. All the imagoes were within six hours of the same age at the start of each experiment, that is to say, within six hours of emergence from the pupal stage. There were 25 units in each experimental series ($25 \times 16 = 400$ beetles). Each unit was examined every fifth day; the deaths recorded that had occurred since the last previous examination; and the dead beetles removed. After each such examination the still living beetles were returned to the appropriate bottles.

In order to avoid rough handling of the imagoes during the long duration of the experiments the flour was not sifted mechanically at the 5-day examinations. Instead the flour from each bottle was spread out and the beetles were then gently removed by hand. Throughout the experiments, so long as it was possible, the population density in each bottle was held constant at the initial level of 16 beetles per bottle. This was done by continually taking beetles from the highest numbered bottle still extant in each series to fill the gaps caused by deaths in the lower numbered bottles in the same series. Thus the first replacements in any particular series came from bottle 25; then from bottle 24 after all the beetles in bottle 25 had been used up in this way; and so on. This procedure resulted in the major part of all the beetles living at the constant density of 16 throughout the greater part of the experiments.

All the bottles were kept in dark incubators at a temperature of $28^{\circ}\text{C. } (\pm 0.5^{\circ})$, and a relative humidity that varied between 40 and 50 per cent.

III

In Table 1 are presented the basic biometric constants describing the variation of *Tribolium* in respect of duration of life. These constants are computed from the observed distributions of deaths, and not from the life table d_x distributions given farther on in the paper.

TABLE 1
BIOMETRIC CONSTANTS FOR LIFE DURATION IN *TRIBOLIUM CONFUSUM*

Sex	Mean (days)	Median (days)	Standard deviation (days)	Coefficient of variability (per cent.)
Males	177.80 \pm 2.83	171.65 \pm 3.54	84.26 \pm 2.00	47.39 \pm 1.36
Females	198.50 \pm 3.48	210.70 \pm 4.36	103.45 \pm 2.46	52.11 \pm 1.54

From Table 1 the following points are to be noted:

1. The average duration of life for the whole 800 beetles in the experiments was about 188 days, or a little more than one half of a year, with a median duration of life only about 3 days longer than the mean, an entirely insignificant difference. This indicates that *Tribolium* is longer lived on the average, and by a large margin, than any other insect for which a life table has yet been computed covering the adult (imago) stage of the life cycle. On the other hand, *Tribolium* is in no way exceptional in respect of either mean or maximum longevity among beetles, as is seen by comparison of the data in Table 1 with those of Blunck (1924) on *Dytiscus* (who found that individuals normally live on the average from one to two years, and exceptionally to as much as 2½ to 3 years), or those of Labitte (1916), as shown in the following list:

MEAN DURATION OF LIFE (IN DAYS) OF VARIOUS BEETLES
(from Labitte)

	Males	Females
<i>Procerustes</i>	374.10	338.20
<i>Carabus</i>	323.20	385.71
<i>Necrophorus</i>	232.33	291.50
<i>Dytiscus</i>	853.66	740.00
<i>Hydrophilus</i>	164.66	374.00

<i>Melolontha vulgaris</i>	19.20	26.81
<i>Cetonia aurata</i>	57.50	88.00
<i>Lucanus cervus</i>	19.16	31.72
<i>Dorcus</i>	327.00	375.33
<i>Ateuchus</i>	338.25	466.80
<i>Sisyphus</i>	198.40	266.50
<i>Copris</i>	496.55	623.44
<i>Geotrupes</i>	700.06	642.14
<i>Oryctes</i>	37.50	55.50
<i>Blaps mortisaga</i>	848.20	914.40
<i>Blaps gigas</i>	700.00	727.66
<i>Blaps magica</i>		
<i>Blaps edmondi</i>		
<i>Akis</i>	854.40	951.42
<i>Pimelia</i>	669.08	714.18
<i>Timarcha</i>	135.00	181.66

2. In neither of the series of experiments does the median duration of life differ from the mean by an amount that can definitely be regarded as statistically significant.

3. In the favorable environmental conditions presented by continually renewed fresh flour the female beetles are longer lived on the average than the males. The mean deficiency in male life duration is $198.50 - 177.80 = 20.70 \pm 4.48$ days, or 10.4 per cent. of the female mean. This difference is 4.6 times its probable error, and may therefore be regarded as statistically significant. This evidence that normally in *Tribolium* the females tend to be longer-lived than the males is in accord with the general rule seen in the case of man (see Hill, 1936, or any other human life tables) and in various lower organisms (see Pearl, 1928). Furthermore it agrees with the findings of Blunck (1924) on *Dytiscus* and of Labitte (1916) on various other species of Coleoptera.

4. *Tribolium* appears to be relatively more variable in respect of duration of life, as imago, when judged by the coefficient of variation, than *Drosophila*, but about equal in relative variability to *Acrobasis*. Under the conditions of continually renewed fresh flour the females appear to be probably significantly more variable in life duration than the males, whether the variation is mea-

sured absolutely (standard deviation) or relative to the respective means (coefficient of variation).

IV

The plan of the experiments on *Tribolium* and the method of record taking were such that each individual beetle was directly observed throughout its lifetime from birth (emergence) to death. Consequently the actuarial methods used in computing the life tables could be direct, without necessity for resort to the postulational and inferential methods that are required in constructing life tables for human populations. The actual procedure followed in constructing the *Tribolium* life tables (Table 3) was first to graduate the observed survivorship distributions, by a technique presently to be described, and from the resulting graduations read off the l_x values at 5 day intervals. From these l_x values the deaths (d_x) in each age interval were got by successive subtraction of the l_x figures. Then the death rates per 1,000 exposed to risk at the beginning of each age interval ($1,000 q_x$) were readily obtained. It was not thought necessary to table the expectations of life for this form.

Inspection of the observed survivorship distributions indicated that no single simple function could be expected to fit satisfactorily such sinuous lines. So it was decided to break the life span up into three parts, namely (i) from age 0 to 70 days; (ii) from age 70 to 110 days; and (iii) from age 110 days to the end of life, and graduate each one of these three portions separately in each case. The first and the second portions were each fitted with a third order parabola, and the final portion by the Gompertz-Makeham formula. The three component curves were then welded at their junction points. The resulting fits were quite satisfactory, though at the extreme upper end of the life span there was the usual roughness consequent upon the meagerness of the experience.

The equations to the curves are set forth in Table 2.

In each case the origin is at 0 and x is measured in 5-day units.

The resulting life tables are given in Table 3, and the survivorship curves shown graphically in Fig. 1. It will

TABLE 2
EQUATIONS OF CURVES USED IN FITTING OBSERVED SURVIVORSHIP OF *TRIBOLIUM*

Sex	Curve for 0-70 days	Curve for 70-110 days	Curve for 110 days to end
Males	$l_x = 1000 - 29.16280x$ $+ 2.709904x^2 - 0.0863800x^3$	$l_x = 1017.52 - 25.850x$ $+ 1.9683x^2 - 0.0567x^3$	$\log_{10} l_x = 7.55567 - 0.0659397x$ $- 4.64763 \times 0.9832230^x$
Females	$l_x = 1000 - 33.13819x$ $+ 2.678403x^2 - 0.0823376x^3$	$l_x = 967.08 - 16.494x$ $+ 0.8043x^2 - 0.0214x^3$	$\log_{10} l_x = 3.02096 - 0.00545333x$ $- 0.00257594 \times 1.0894648^x$

be understood that in each of the series in Table 3 the l_x and d_x values towards the end of the life span required adjustment as usual, and the figures tabled represent the rounding off into whole numbers, following the usual convention, of what are really fractional values in the detailed work sheets. This process of rounding off fractional values results in the sum of the d_x figures as printed sometimes not exactly equalling 1,000 in the tables.

From the data presented the following results appear:

1. The life tables show that the dying out of *Tribolium* displays in a definite and striking manner a feature not hitherto found in the life table for any lower organism, namely a relatively heavy rate of mortality at the beginning of imaginal life. This obviously corresponds, in respect of its time in the life cycle and manner of incidence, to the infant and early childhood mortality so characteristic of human life tables. We are inclined to the view that the principal causal factor concerned in producing this heavy mortality at the beginning of the imaginal life span is probably innate and largely genetic. On this view these beetles dying off in the first month or so of life may be assumed to represent the biologically "bad eggs," in the sense that they may be regarded as individuals of defective biological organization such that, while they were able to survive through egg, larval

and pupal states, they could not go on living much longer thereafter. Their deaths, on this hypothesis, may be taken to represent chiefly the initial eliminations by natural selection in the imago stage of the life cycle. The age of lowest death rates during the life span, which may be taken as indicating the point at which this tentatively postulated first selective elimination of individuals defectively organized innately has come to an end, falls in the age class 50-55 days in all four life tables. Thereafter

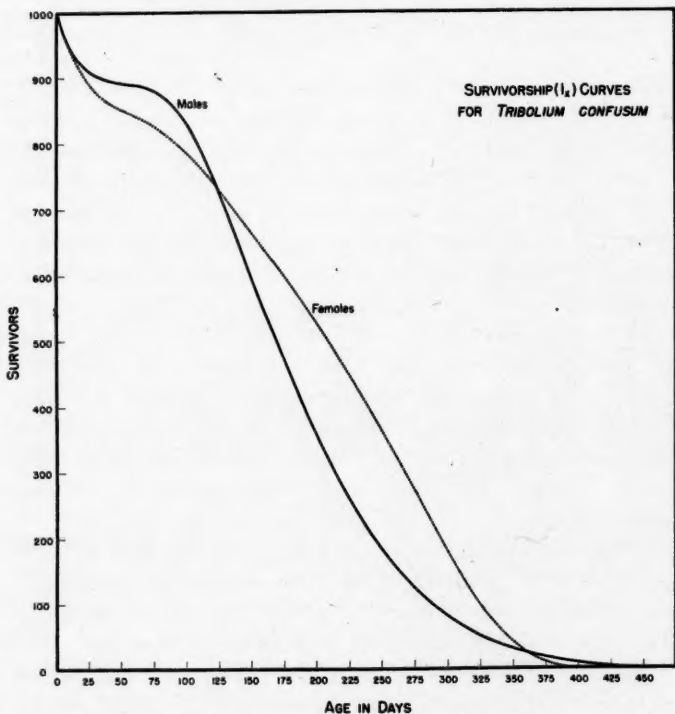


FIG. 1. Survivorship lines (l_x) for *Tribolium* life tables. Data from Table 3.

the death rates steadily rise, with some minor fluctuations, until the last individual has died at the upper end of the life span.

TABLE 3
LIFE TABLES FOR TRIBOLIUM CONFUSUM
A. Males reared in fresh flour

x (days)	l_x	d_x	$1000 q_x$ (per 5 days)	π Age (days)	l_x	d_x	$1000 q_x$ (per 5 days)	π Age (days)	l_x	d_x	$1000 q_x$ (per 5 days)
0-5	1000	27	26.5	180-185	451	24	52.7	300-365	97	3	94.0
5-10	973	25	22.2	185-190	427	23	54.5	305-370	22	3	94.8
10-15	952	17	18.1	190-195	404	22	55.8	370-375	22	2	95.6
15-20	935	13	14.3	195-200	382	21	57.3	375-380	20	2	96.4
20-25	921	10	10.9	200-205	360	21	58.8	380-385	18	2	97.1
25-30	911	7	7.9	205-210	339	20	60.2	385-390	16	2	97.9
30-35	904	5	5.4	210-215	318	20	61.6	390-395	15	1	98.7
35-40	898	3	3.5	215-220	299	19	63.0	395-400	15	1	99.4
40-45	896	2	2.5	220-225	280	19	64.5	400-405	13	1	100.1
45-50	894	2	1.2	225-230	262	17	67.7	405-410	11	1	100.8
50-55	893	1	1.0	230-235	245	16	67.0	410-415	10	1	101.5
55-60	892	1	1.3	235-240	228	16	68.3	415-420	9	1	102.1
60-65	891	2	2.2	240-245	213	15	69.6	420-425	8	1	102.8
65-70	889	3	3.7	245-250	198	14	70.9	425-430	7	1	103.5
70-75	886	5	5.1	250-255	184	13	72.1	430-435	6	0	104.1
75-80	881	6	6.3	255-260	169	12	73.3	435-440	5	0	104.7
80-85	876	7	8.2	260-265	158	12	74.6	440-445	5	0	105.4
85-90	868	9	10.4	265-270	146	11	75.6	445-450	5	0	106.0
90-95	859	11	13.1	270-275	135	10	76.7	450-455	4	0	106.6
95-100	848	14	16.2	275-280	125	10	77.9	455-460	4	0	107.1
100-105	834	17	20.0	280-285	115	9	78.9	460-465	3	0	107.7
105-110	818	20	24.3	285-290	106	8	80.0	465-470	3	0	108.3
110-115	798	22	27.7	290-295	98	8	81.1	470-475	3	0	108.9
115-120	773	23	31.7	295-300	90	7	82.1	475-480	2	0	109.5
120-125	753	25	35.5	300-305	82	6	84.1	480-485	2	0	109.9
125-130	729	25	33.6	305-310	75	6	84.1	485-490	2	0	110.5
130-135	704	25	35.5	310-315	69	6	85.1	490-495	2	0	111.0
135-140	679	25	37.4	315-320	63	6	86.1	495-500	1	0	111.5
140-145	654	26	39.2	320-325	58	5	87.0	500-505	1	0	112.0
145-150	628	26	41.0	325-330	53	5	87.9	505-510	1	0	112.5
150-155	603	26	42.8	330-335	48	4	88.8	510-515	1	0	113.0
155-160	572	26	44.5	335-340	44	4	89.6	515-520	1	0	113.5
160-165	551	25	46.3	340-345	40	4	90.6	520-525	1	0	113.9
165-170	525	25	47.9	345-350	36	3	91.5	525-530	1	0	114.4
170-175	500	25	49.6	350-355	33	3	92.4	530-535	1	0	114.8
175-180	475	24	51.2	355-360	30	3	93.2	535-540	1	1	115.3

TABLE 3 (Continued)
LIFE TABLES FOR TRITOLIUM CONFUSUM
B. Females reared in fresh flour

Age (days)	l_x	d_x	1000 q_x (per 5 days)	Age (days)	l_x	d_x	1000 q_x (per 5 days)	Age (days)	l_x	d_x	1000 q_x (per 5 days)
0-5	1000	31	30.5	145-150	679	13	18.7	290-295	216	18	85.1
5-10	969	26	26.5	150-155	666	13	19.3	295-300	197	18	91.3
10-15	944	21	22.6	155-160	653	13	19.9	300-305	179	18	98.1
15-20	922	17	18.9	160-165	640	13	20.6	305-310	162	17	103.4
20-25	895	14	15.5	165-170	621	13	21.3	310-315	145	16	109.7
25-30	864	11	12.5	170-175	600	14	22.0	315-320	128	16	115.7
30-35	830	9	10.0	175-180	587	14	22.9	320-325	113	15	121.7
35-40	871	7	7.9	180-185	573	14	23.9	325-330	98	14	127.0
40-45	864	5	6.3	185-190	558	14	24.9	330-335	84	13	132.3
45-50	859	5	5.3	190-195	544	15	26.0	335-340	71	12	137.6
50-55	854	4	4.9	195-200	529	15	27.2	340-345	60	10	142.9
55-60	850	4	5.0	200-205	514	15	28.5	345-350	49	9	148.2
60-65	841	3	3.7	205-210	493	16	31.4	350-355	39	8	153.5
65-70	835	3	7.0	210-215	483	16	33.2	355-360	32	7	158.8
70-75	828	7	8.0	215-220	467	16	35.0	360-365	25	6	164.1
75-80	821	7	8.4	220-225	451	17	36.9	365-370	19	5	169.4
80-85	814	8	9.1	225-230	434	17	39.1	370-375	14	4	174.7
85-90	806	9	9.8	230-235	417	17	41.4	375-380	10	3	180.0
90-95	797	10	10.8	235-240	400	18	44.0	380-385	7	2	185.3
95-100	785	10	12.9	240-245	384	18	46.8	385-390	5	2	190.6
100-105	777	12	14.9	245-250	364	18	49.8	390-395	3	1	195.9
105-110	766	12	15.9	250-255	346	18	53.0	395-400	2	1	201.2
110-115	753	12	16.2	255-260	328	19	56.6	400-405	1	0	206.5
115-120	741	12	16.6	260-265	309	19	60.4	405-410	1	0	211.8
120-125	729	12	16.9	265-270	291	19	64.6	410-415	1	0	217.1
125-130	717	12	17.3	270-275	272	19	69.1	415-420	1	0	222.4
130-135	704	13	17.8	275-280	253	19	74.0	420-425	1	0	227.7
135-140	692	13	18.2	280-285	234	19	79.4	425-430	1	0	233.0
140-145				285-290				430-435		1	238.3

2. Following this quasi-infant mortality component the l_x curves decline at a slow rate up to 80 or 90 days of age (few deaths per age interval), and thereafter to the end of the life span go smoothly down with a steeper slope until near the terminal points.

3. Among the beetles living in regularly renewed fresh flour, which may be regarded as representing optimal environmental conditions in which normal relationships may reasonably be expected to appear, the females (Table 3B) show a *higher* death rate (1,000 q_x) than the males (Table 3A) at all ages from emergence up to 85 days. But in the period from age 85 days up to 290 days the female death rates are uniformly *lower* than the male. Finally from 290 days on to the end of the life span the female rates are again uniformly higher, age for age, than the male rates. But at age 290 days there are left but 98 male and 216 female survivors out of the 1,000 starting at emergence in each case. Altogether it is clear that the females owe their superior average longevity over the males to their lower death rates over the whole of what may be roughly called their middle period of life.

V

The similarity of the *Tribolium* life tables to those for man in respect of the exhibition of an "infant mortality" component has already been noted. A more detailed comparison may now be undertaken. In carrying this out the method used by Pearl and Miner (1935) will be employed. Briefly this method consists of scale alterations based upon equating *mean* durations of life and expressing absolute ages as percentage deviations, plus or minus, from the respective absolute mean ages of the forms compared.

Table 4 and Fig. 2 set forth the results of this procedure as applied to (a) the life tables for *Tribolium* males and females living in regularly renewed fresh flour (Tables 3A and 3B *supra*), and (b) Hill's (1936) tables for white males and white females in the United States

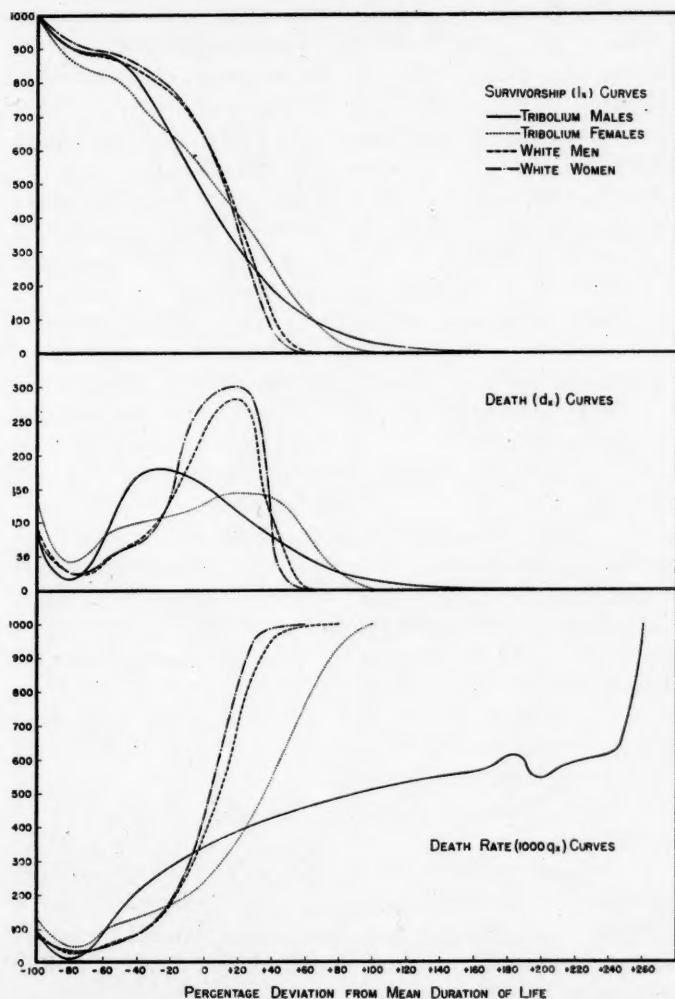


FIG. 2. Survivorship, death and death rate curves for *Tribolium confusum* and man on a relative time base. In each case the mean duration of life is taken as 100 per cent. on the abscissal scale, and all other ages (time durations) are expressed as percentage deviations (plus or minus) from this mean. It is to be noted that the scale of plotting the ordinates of the death (d_x) curves is double that for the survivorship and death rate curves.

1929-31. In the case of the human life tables the expectation of life at birth is taken as the mean duration of life in each case. In the case of *Tribolium* the means are given in Table 1.

The fundamental similarity in form of the *Tribolium* life curves and those for man is evident. The only important difference between them is found in the much greater variation exhibited by the death (d_x) curves in *Tribolium* as compared with the human. The *Tribolium* d_x curves not only have a greater range of variation, but are much flatter over the major portion of their course. *Tribolium* has a very wide ratio of total life span to mean duration of life. In the males this ratio is about 304:100, and in the females 219:100. For the human life tables the corresponding ratios are 179:100 and 169:100.

A comparison of Table 4 with Table 7 of Pearl and Miner (1935) and of Fig. 2 with Figs. 1, 3 and 5 of the same paper makes it clear that the *Tribolium* life table curves conform much more closely to the human pattern (with the differences just noted) than to that characteristic of any of the lower organisms for which life tables have as yet been computed. It is interesting to note that, in the notation of the (1935) paper the d_x curve for *Tribolium* males is of the B_2 fundamental type while that for the females is of the B_1 type, with, of course, an "infant mortality" component added at the beginning in both cases. Human d_x curves are characteristically of the B_1 type.

The comparative forms and shifts of the human male and female life table curves when put upon a relative instead of an absolute time base are of interest, because at first glance they appear paradoxical. At all absolute ages up to 101 years the life table death rates are smaller for women than for men. But when ages are expressed as percentage deviations from the respective mean durations of life (e_x) this is true only for minus deviations of greater numerical magnitude than roughly about -20 per cent. (i.e., deviations of -40, -60, -80, and -100

per cent.). For deviations from the respective male and female mean durations of life of -20 , 0 , $+20$, $+40$ and $+60$ the death rate per 20 per cent. deviation is greater for the females than for the males, with correlative shifts in the other life table functions. This result comes about from the greater mean duration of life of the human female as compared with the male, which causes corresponding *percentage* deviations to be associated with higher absolute ages.

VI

SUMMARY

In this paper are presented life tables for males and for females of the beetle *Tribolium confusum* Duval, living in regularly renewed fresh flour. The *Tribolium* life curves resemble in their fundamental pattern human life curves more closely than do those of any other organism for which life tables have as yet been computed. They have at the beginning of life in the imago stage a component corresponding in the time and quantitative relations of its incidence to the infant mortality component of human life tables.

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THE RECAPITULATION THEORY OR BIO-GENETIC LAW IN EMBRYOLOGY*

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ONE hears to-day in conversation or reads not so infrequently that modern study "has brought the Biogenetic Law into disrepute" (Ashley-Montagu, 1938).¹ In the face of such criticism it is worth while now and then to pause and consider the real nature and actual status of this law, or as it is so much better styled, recapitulation theory, the roots of which go back into the early years of the nineteenth century.

There can be no real disagreement as to the observable facts on which the theory is based, although in general propositions there is sometimes overstatement and, in cases, an admixture of theory. Among the early writers J. F. Meckel in various passages of his "Comparative Anatomy" discusses the process in question. Thus he writes (1821: 396):² "The development of the individual organism follows the same laws as the development of the whole animal series, that is, the higher animal in its individual developments runs through in essentials the permanent stages below it." He does not mean all the stages, *i.e.*, all the lower groups but only some (*loc. cit.*, p. 9) which he designates as the most preferable ("die vorzüglichsten der Stufen"). Into this "vorzüglich" we of to-day, asking why certain stages have been preserved

* The manuscript of this paper was completed in longhand by the author and marked "for publication." In a few places where the meaning would undoubtedly have been clarified by the author had he had opportunity to see the typewritten copy made after his death, colleagues in the Department have made inserts or changed certain words or phrases. All such alterations are enclosed in brackets. Quotations from German authors which occur so frequently in this paper are given in Professor Wilson's MS translation. To avoid frequent repetition, this fact is not mentioned in connection with each quotation.

R. E. F.

¹ M. F. Ashley-Montagu, SCIENCE, 87: 2264, 462, May 20, 1938.

² J. F. Meckel, "System d. vergl. Anatomie," erster Theil. Halle. 1821.

in ontogeny, might read subtleties, but, if there, they are no more than shadows.

Meckel, like most others of his time, is not seriously concerned in such matters with the idea of genetic evolution and heredity, although the thought is there in his mind (p. 62). He is content to find principles, an order, in the behavior of living things, rather than explanations (p. 328): "Another internal cause of multifariousness seems to be the impossibility of reaching at once the highest degree of differentiation and consequently the necessity of running through a more or less intricate series of formative stages."

Von Baer's precise statement (1828)³ concerning resemblances between embryo and lower adult is familiar; these resemblances exist because "the least differentiated animal forms depart but little from the embryonic condition and hence retain some similarity to the embryos of higher animal forms" (quoted from O. Hertwig, 1906: 166).⁴ But it is clear, and evident from this very quotation, that Von Baer realizes that resemblances to a lower embryo after the latter has taken on the fundamental structure of the adult are resemblances to the adult. The notochord, myotomes, visceral pouches, some breaking to the exterior as gill slits, twisted tubular heart, aortic arches and simple bilateral venous system, constitute resemblances, and fundamental ones, to adult selachian fish, or, with respect to particular features, in greater degree to cyclostomes and amphioxus.

If we recognize that Meckel has in mind "essentials" of anatomy, there is no difference of any great significance between his statement and that of Von Baer. And Metschnikoff (1886: 126)⁵ in speaking of the point says that Von Baer ultimately came to this conclusion himself.

³ Karl Ernst Von Baer, "Ueber Entw. geschichte d. Thiere," Th. 1. Königsberg. 1828.

⁴ Oskar Hertwig, "Handb. d. vergl. u. exper. Entw. lehre d. Wirbeltiere," Bd. III (3). 1906.

⁵ Elias Metschnikoff, "Embryologische Studien über Medusen." Wien (trans. in part in *AM. NAT.*, April and May, 1887). 1886.

Louis Agassiz in his published lectures on embryology 1849)⁶ also emphasizes the order that is found in nature. The particular part of this order with which he is concerned is the "natural scale" of animals from low to high within a great group, together with the necessity for members of the group in the course of their individual development from the egg to pass along or through this scale. Taking the frog as an illustration (*loc cit.*, 10), he shows that in the course of its larval development it passes through stages in which it successively resembles different lower amphibia. The "natural scale" is in fact revealed in the development of the higher forms of this group (p. 103). Every member of the group "when reproducing its species, passes through these different changes—the higher one through more of the changes; the lower one, undergoing only the earlier modifications" (p. 11). The passage quoted above from Von Baer seems to imply the same idea, that for each great group there is one ontogenetic path along which all must go for a lesser or greater distance. This idea receives some modification later.

The famous three-fold parallelism between the succession of forms in geological time, the gradation of existing animals from low to high and the succession of stages through which the higher members of a group pass in their individual development is explicitly maintained for the echinoderms as a type case showing "that structure, development, and order of succession in time are regulated by one and the same unique principle" (p. 26). Comprehensive statements of this parallelism are made farther on (pp. 102-104).

Agassiz in his general propositions may overstate the degree of resemblance between embryo or larva, existing adult form and fossil form. His illustrative examples show, however, that the agreement he has in mind is usually, at any rate, one of architectural plan. Thus

⁶ Louis Agassiz, "Twelve Lectures on Comparative Embryology." New York, Boston, Philadelphia. 1849.

when he assigns to the bird embryo "even the fins which characterize the fish" (p. 96), he shows (pp. 101-102) the early paddle-like limb previous to segmentation and outgrowth of the digits.

In his later "Essay on Classification" (1857)⁷ Agassiz gives a more permanent form to his ideas on embryonic repetition, the three-fold parallelism and classification. He is only slightly interested in proximate, physiological causes of morphological resemblance and change. Like Meckel he sees in Nature, above all else, conformities to law (*Gesetzmässigkeiten* of German writers). For the explanation of these he goes immediately to a final cause, the Supreme Intelligence (*loc. cit.*, pp. 4, 8 *et pass.*) planning Nature as we find it. He argues against a crude notion of the action of proximate causes, a notion which must have had some currency at the time, *viz.*: the idea that the physico-chemical forces of the environment might of themselves directly produce the peculiarities of existing living things, as if they were rocks or crystals, whereas the facts indicate plainly, he thinks, that the living world is the direct realization of a divine plan (pp. 9, 13, *et pass.*).

Agassiz is deeply and widely interested in the observable facts on which his generalizations rest. The resemblances of embryos to lower forms are for him realities, although not identities, and they call for investigation: "there remains still a wide field of investigation to ascertain the different degrees of similarity between the successive forms an animal assumes until it has completed its growth and the various forms of different kinds of full-grown animals of the same type; between the different stages of complication of their structure in general and the perfect structure of their kindred" (p. 84). He means "kindred," as do O. Hertwig and some others, in a systematic, not a genetic sense.

He recognizes, too, as did Meckel, that while embryos

⁷ Louis Agassiz, "Essay on Classification," in *Contrib. Nat. Hist. of U. S. of America*, Vol. 1. Boston. 1857.

repeat features of lower members of the group, embryos of the higher forms do not offer resemblance to all the lower members, since animals do not form a single simple series. "There remains, therefore, only for us to show now within what limits the natural gradation, which may be traced in the different types of the animal kingdom, corresponds to the changes they undergo during their growth" (p. 119), and he proceeds to examples.

The three-fold parallelism is again emphasized in general propositions (p. 134) with illustrative examples (pp. 119-120). There is "parallelism between the order of succession of animals and plants in geological times, and the gradation among their living representatives," and, again, there is "parallelism between the order of succession of animals in geological times and the changes their living representatives undergo during their embryological growth." (p. 134). We would to-day make less sweeping and more circumstantial statements, perhaps, because the very multiplicity of details may make us hesitate to decide what facts in any particular case are the most significant. But the details need not obscure the great truth in Agassiz's picture, as brought out by well-known examples.

While the recapitulation idea, as a generalization of facts as we find them, long antedated the Darwinian period, there came with the publication of the "Origin" in 1859⁸ the stimulating thought that this phenomenon of repetition, so general in its occurrence and so uniform in its basic character as to be evidently a case of conformity to law, might be the result of a proximate and physiological cause, [namely] heredity. The thought emanating from Darwin's book was soon followed by a definite formulation of the recapitulation theory as an evolutionary explanation of the facts. Fritz Müller (1864)⁹ applied the idea to the life-cycles of crustacea

⁸ Charles Darwin, "The Origin of Species." London. 1859.

⁹ Fritz Müller, "Für Darwin." Leipzig. (Engl. Trans. "Facts for Darwin," 1869. London.) 1864.

and writes (Engl. trans. 1869: 112): "In the second case the entire development of the progenitors is also passed through by the descendants, and . . . the historical development of the species will be mirrored in its developmental history." Haeckel too recognized (1866)¹⁰ this type and later designated it (1874)¹¹ as "palingenetic." Müller considers also the shortening of, and the deviations from, the hereditary path, and so writes (Engl. trans. 114): "The historical record preserved in developmental history is gradually effaced as the development strikes into a constantly straighter course from the egg to the perfect animal, and it is frequently sophisticated [modified or altered] by the struggle for existence which the free-living larvae have to undergo." These [latter] phenomena, which seem to be universally present in ontogeny, were set out also by Haeckel (1866) who (1874) applied to them the term "caenogenetic."

Haeckel, in his "Prinzipien" (1866) and in later writings and special investigations, made the recapitulation theory a very active force in the whole of biology, designating it as the Biogenetic Law (*biogenetisches Grundgesetz*, term introduced 1872, p. 467).¹² Among his "theses" (1866: 300) on the causal connection between ontogenetic and phylogenetic development is the intriguing and sometimes misleading formula: "Ontogeny is the brief and rapid recapitulation of phylogeny" and the more flexible statement: "The organic individual repeats during the rapid and brief course of its individual development the most important of those changes in form which its ancestors . . . went through." Forty-four years after the publication of the *Prinzipien* Haeckel speaks (1910: 22),¹³ and with justice, of the stimulating,

¹⁰ Ernst Haeckel, "Prinzipien d. gen. Morphologie d. Organismen." Berlin. 1866.

¹¹ Idem, "Anthropogenie oder Entwicklungsgeschichte des Menschen." Aufl. 1. Leipzig. 1874.

¹² Idem, "Die Kalkschwämme," Bd. 1. Berlin. 1872.

¹³ Idem, "Anthropogenie," Aufl. 6, erster Teil. Leipzig. 1910.

extensive and profound influence the biogenetic law has had on research, and of its many critics, and correctly says: "No opponent of the principle has been able to set up anything better in its place." Some of the criticisms have been due to misunderstanding and this has probably been made easier by Haeckel's insistence on the use of the word "mechanical." "Phylogenesis," he says, "is the mechanical cause of Ontogenesis" (1877: 7¹⁴; 1910: 22); whereas the mechanical (a poor word at the best) phenomena are the local cell proliferations, fusions, absorptions, cell movements and changes of shape [which are] details in the formation of the repetitions we are considering. Some, strange to say, see only these [details], but that is to leave the larger problem quite untouched, the problem of what sets in motion all this detailed activity. Criticism has frequently been called out, not as to the truth of the principle, but as to its application at times in the construction of elaborate and detailed phylogenies.

The evolutionary explanation, however true it may be, and the generalization to which it is applied are distinguished by careful writers. Thus in a well-known university text of that period Claus (1880: 111)¹⁵ writes: "Many examples demonstrate the truth of the principle that the successive developmental phases of embryonic life mirror features of simpler and lower groups or of more perfectly organized groups" [referring to cases where the life cycle is one of degeneration] "of the same type" [phylum]. And in one of our recent texts of similar character R. Hertwig (1931: 43)¹⁶ says: "Every animal runs through in essentials in the course of its development the stages which are retained permanently in lower or, correctly speaking, more primitively organized animals of the same great group." And this conformity to law (*Gesetzmässigkeit*) is one "which at

¹⁴ Idem, "Studien zur Gastraea-theorie." Jena. 1877.

¹⁵ Carl Claus, "Grundzüge d. Zoologie," Aufl. 4, Bd. 1. Marburg. 1880.

¹⁶ Richard Hertwig, "Lehrb. d. Zoologie," Aufl. 15. Jena. 1931.

present can only be explained historically, that is, through the assumption of a common descent." Oskar Hertwig's criticism (1906: 149-180) of the biogenetic law is especially significant as coming from one so eminent in embryology and is moreover of the highest importance in that it brings out the essentials of whatever has been said against the law in the many discussions of the subject. Hertwig finds that no true picture of an ancestral form can be gained from ontogeny (*loc. cit.*, 169) nor from comparative anatomy (p. 176). The embryonic stages are only outline sketches that tell us nothing of the particulars that go to make up a real animal, and no one would maintain that any existing simpler form, amphioxus, *e.g.*, is in the ancestral line of a higher form. Often too there is such an intermixture (p. 174) of lower and higher characteristics that the embryonic stage can not be said to represent an ancestor.

This objection then is that an embryonic stage is never the repetition, through and through (p. 166), of an ancestral form or organ. It is only a phase in a continuous change that will end in an animal very different from the hypothetical ancestor. A gastrula, for instance, is never a hydroid polyp, although it may differ externally from one "only in insignificant features." No fish, he goes on, constructed as is the embryo of a higher vertebrate, could have existed (p. 167). The notochord of a mammalian embryo is not a replica of the amphioxus notochord since it is not really a supporting organ (p. 169).

Of course all this is true, but it is directed against a very literal interpretation of the statement that ontogeny is a recapitulation of phylogeny. Such an interpretation would demand not resemblance but identity of the embryonic stage with the lower adult, whereas in both generalization and theory the mind is directed to a general resemblance, not to a detailed one, and to organs, sometimes whole systems of correlated organs, more often than to the embryonic body as a whole. That is our meaning in practice when we speak of a "fish-like stage."

In general propositions, to be sure, from Meckel to R. Hertwig, we may refer to the whole body, but the examples show that what is had in mind is often only some organ or system of organs such as the visceral clefts and arches, simple heart, and arterial arches of the mammalian embryo (R. Hertwig, *loc. cit.*, 43, 45).

It is for these resemblances of basic morphology between embryo and lower adult, marvelous enough, that we ask an explanation. Oskar Hertwig's explanation (p. 178) is that there are basic morphogenic laws which bring about the facts as we see them. The first bits of protoplasm that were formed on the earth were cells (p. 177). From these there arose polyphyletically, *i.e.*, independently of one another, various lines or great groups of organisms (pp. 165, 177). Through the operation in them of the same morphogenic laws, similarities which we call homologies were produced (pp. 173, 179). In ontogeny the stages which succeed one another are necessitated by these laws. Ontogenetic stages thus can not be eliminated if the end result, the adult condition, is to be reached. They provide the necessary conditions for the attainment of this objective (p. 173). And Hertwig does not [refer in this connection to] an actual concrete case where of course the path is fixed, relatively speaking, and [fixed], as very many suppose, by heredity, but [he refers to development] in the abstract. That is, the formation of these preliminary stages is a method which must be pursued in the nature of things if a complex body is to be built up out of a cell. This idea is discussed (*loc cit.*) for some of the first and simplest steps in ontogeny to which it may be applied with the appearance of probability, although even here diversity in the actual methods employed by different animals, as in the development of a two-layered stage (Metschnikoff, 1886), shows that there is no one morphogenetic path along which it is necessary for all to move. Basic structural similarities, he thinks, need not therefore be taken to indicate genetic relationship (pp. 171, 176, 179) any

more than the similarity between crystals which arise out of the same solution (p. 180) need be taken to indicate that they arose from some preceding crystal.

The objection to all this is: in the first place, it is incredible that the circuitous course of ontogeny, as for instance in the development of the arteries in bird or mammal, is brought about by morphogenic laws of semi-mechanical nature, comparable with those operative, for example, in eggs where the character of the segmentation is determined by the distribution and amount of yolk (p. 172), a fact that may be inferred from comparative study and is demonstrable in O. Hertwig's well-known experiment of centrifuging the frog egg and so causing it to segment in meroblastic fashion (1897);¹⁷ and, secondly, nothing is added to the observable facts except the idea that there is something unknown in protoplasma which makes them as they are. For that something which brings about these intricate resemblances between embryo and lower form the only explanation we have to-day, it would seem, remains, as R. Hertwig says (*loc. cit.*, 43), the evolutionary one, the idea of a common descent.

To many, however, facts summed up in generalizations are more important than any explanatory theory. O. Hertwig in his essay brings out this idea strongly, emphasizing that the homologies between adult organisms and between embryos and lower forms are anatomical concepts independent of all theory. It is reassuring to know that the generalization which has been handed down since Meckel's time and which underlies the recapitulation theory of Müller and Haeckel, is a well-based one, summing up, as it does, very many cases of ontogenetic repetitions, usually imperfect of course, of structures that are functional in lower or less specialized forms.

As to the evolutionary explanation, heredity need not, we know, continue to follow a fixed path. Why, then, we

¹⁷ Oskar Hertwig, "Ueber einige am befruchteten Froschei durch Centrifugalkraft hervorgerufene Mechanomorphosen." *Sitz.-Ber. Königl. preuss. Akad. Wiss.*, Berlin. 1897.

may ask, have certain ancestral features been retained in particular organisms? Is it because of the inertia of heredity or have such structures proved their worth as adaptive mechanisms? Astonishing if some of them have, so indirect and complicated is the path to the end-term, the adult state. If interest in comparative embryology ever reawakens this question may come to the fore with a renewed study of naturally occurring caenogeny and a determined effort to reproduce experimentally and abundantly such morphogenic differences between members of a group.

RELATIONSHIPS OF THE ACANTHOCEPHALA¹

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PROBLEMS concerned with the origin and the relationships of the Acanthocephala have received but little attention at the hands of investigators. The usual avenues for directing inquiries into phylogeny yield but scanty convincing evidence of direct relationship between the Acanthocephala and other animal groups. The reasons for this condition are found in the specialization which has accompanied perfect adaptation and complete organic adjustment to the parasitic existence. Many other parasitic organisms, through either their anatomy or their ontogeny, reveal indisputable evidences of relationship with free-living forms which occupy a natural position in the scheme of classification. Thus the cestodes and the trematodes, in spite of adjustments to parasitic life, display unqualified affinities with the free-living Turbellaria. Similarly, the highly modified crustacean parasites such as some of the parasitic copepods and isopods and the classical example, *Sacculina*, through their larval stages provide adequate proof not alone of the phylum to which they pertain but, at the same time, present the evidences that permit of their being placed in a definite, natural scheme of alignment with closely related free-living genera. Thereby, coordination of conspicuously specialized with unmodified forms becomes possible down through not only the class and the order but frequently to the category of family or even of genus. Such possibilities are wholly lacking for the Acanthocephala, for the entire group stands apart in a condition of isolation that has baffled most investigators who have given thought to the problem. Agreement is even lacking

¹ Contributions from the Zoological Laboratory of the University of Illinois, No. 545.

as to the phylum of the animal kingdom to which this group shows closest relationship.

For more than half a century, general treatises on zoology have rather uniformly adopted the policy of affiliating the Acanthocephala with the Nematoda and the Gordiacea in an unnatural assemblage, the Nemathelminthes, wherein the chief cohesive element has been the negative evidence of lack of outstanding distinctive characters, bolstered by the questionably valid direct evidence of superficial resemblance in monotomy of external form. This position so forcibly recalls the qualifications for admission to the class Vermes of Linnaeus that to question its validity calls for no extended defense.

In 1848, Leuckart considered the cestodes and Acanthocephala as the two coordinate orders comprising his class Anenteraeti. In so doing, he was one of the early investigators to recognize common lines of descent running through these two groups. Unfortunately, his procedure in placing trematodes, turbellarians, leeches and nemertines into one class furnishes basis for doubting the meaningfulness of his classification.

As early as 1891, Otto Hamann directed attention to certain resemblances between the embryos of Acanthocephala and those of Cestoda. He called attention to the flattened body in the larger species and to the pseudometamerism (1891: 3) present in Moniliformis and many other larger forms though he deemed these likenesses superficial. It was in connection with a description of the gastrula stage that Hamann made his first significant comparison between Acanthocephala and Cestoda when he referred to their common possession of a central cell mass, the entoblast and a single-layered ectoblast.

In so far as the present writer is aware, this is the first substantial evidence throwing doubt upon the widely prevalent view of Acanthocephala as roundworms. Throughout this same article, Hamann, lacking the ardor of a protagonist, makes numerous comparisons showing how nuclear behavior and musculature in the Acantho-

cephala agree with conditions found in the nematodes. Though his observations furnish the basis for later direct comparisons between Acanthocephala and the Cestoda, Hamann seems to have been unwilling to press his observations beyond the point of calling attention to similarities and differences.

In a Russian article, with a brief summary in German, N. Cholodkovsky (1897) gave the first critical analysis of the evidences of the phylogenetic relationships of the Acanthocephala. He summarized his conclusions with the terse pronouncement that the Acanthocephala have nothing in common with the roundworms. In a series of brief comparisons Cholodkovsky called attention to the following points wherein the Acanthocephala resemble the Cestoda: (1) the development of the several-layered musculature, (2) the absence of a digestive system, (3) the presence of a thin cuticula, (4) the occasional appearance of a protonephridial excretory organ, and several lines of evidence from embryology, particularly (5) the nature of the embryonic membranes, (6) the provisional hooks of the embryo, (7) development of the bulk of the body from a central embryonic cell mass, and (8) the migration of the embryos. In summarizing, Cholodkovsky states that all the above likenesses give evidence that the Acanthocephala and Cestoda have had a common origin and that the former "must thus be placed in the system, either as an independent class beside the cestodes or as an appendix to the flatworms, not to the nematodes."

In 1924, the present writer presented a paper on the relationships of the Acanthocephala before the American Society of Parasitologists in which the similarities between cestodes and acanthocephalans were stressed, but only an abstract of this paper has been published (Van Cleave 1924: 119). Except for this one reference, the outspoken dictum of Cholodkovsky has received little recognition. It is the purpose of the present paper to review again the evidences and to extend the observations still further.

Several writers have questioned the assignment of Acanthocephala to the roundworms but have offered nothing as an adequate substitute. Lankester in the eleventh edition of the "*Encyclopaedia Britannica*" (Vol. 1, p. 110) defines the Acanthocephala as "a compact group of cylindrical, parasitic worms, with no near allies in the animal kingdom." In a summary of the classification adopted for the "*Encyclopaedia Britannica*" (Vol. 28, p. 1035), the Acanthocephala are designated as one of five invertebrate phyla listed following the classification of the Vertebrata. Similar noncommittal treatment has been accorded the group by several recent writers, particularly by authors of elementary text-books, who have avoided controversy by listing the Acanthocephala as one of the "problematical" groups, showing no direct evolutionary relationship with any other present-day group.

Some recent treatises have placed all the worms in a single group, nearly the equivalent of Linnaeus' Vermes, but few American zoologists have adopted this solution of the matter.

Meyer (1932-3: 520) has assembled the Rotifera, Gastrotricha, Kinorhyncha, Priapulioidea, Acanthocephala, Nematomorpha and Nematoda into a group which he designates as the Aschelminthes. As a cohesive feature he finds in all of these the division of the body into a praesoma and a metasoma of which the former consists of a hemispherical apical region and a primarily adoral neck region. Further comparisons become highly speculative when Meyer attempts to establish homologies on conjectural grounds. The type of cleavage common to the Rotifera and the Acanthocephala, which he mentions as significant, is doubtless an important point of agreement. In both the Acanthocephala and the Rotifera, determinate cleavage leads to the establishment of fixed numbers of nuclei at least in some of the representatives of both groups though the present writer has shown (Van Cleave, 1928) that in

normal ontogeny of the Acanthocephala this basic plan of cell constancy becomes masked by a superimposed amitotic fragmentation of nuclei in many genera. Likewise, even in the most rigorous examples of cell constancy in the rotifers, as exemplified by *Hydatina senta*, senescence may impose a secondary phase of inconstancy upon a basic plan of absolute nuclear pattern at the close of the ontogenetic processes (Van Cleave, 1922). Significant as the agreement of Acanthocephala and Rotifera in details of cleavage may seem, it is no more significant than the close harmony between cleavage patterns in the Annelida and the Mollusca, yet this point of agreement is not seriously advanced as brief for including the molluscs and annelids in the same phylum. Possession of characters in common, points to possibilities of common ancestry and common line of descent but offers no proof of identity in taxonomic status which would necessitate including the forms in the same phylum.

Hatschek previously advanced a grouping somewhat similar to that of Meyer, but of broader scope, when he proposed a phylum Scolecida to include the flatworms, rotifers, endoprocts, nematodes and acanthocephalans. His system had the definite advantage of being based on anatomical and promorphological likenesses though protonephridia which he considered as basic for this aggregation are lacking in the nematodes.

When obvious relationships are lacking, possible avenues of descent must be scanned with care. Most evidences of acanthocephalan relationship brought forward in the past have been based on superficial characters. The cylindrical form of the body mentioned by Lankester and commonly invoked as an evidence of roundworm affinities is, in reality, an artifact. In the lumen of the host intestine the acanthocephalan body is in many species collapsed and distinctly flattened. Students who have studied preserved specimens, observe the worms in a turgid state which accompanies removal to fluid for examination or to killing and preserving reagents.

In attempting to review the evidences of relationships of the Acanthocephala, it soon becomes obvious that the usual avenues for seeking evidences of phylogenetic relationships are seriously obstructed. Paleontology, which has furnished incontestable evidence in many instances where morphology and ontogeny fail to yield conclusive evidence, has had a weak voice in directing the search for evidence of the origins of the Acanthocephala.

Indirect evidence points to the fact that the group of Acanthocephala is older than the present-day fauna, the species of which serve as hosts to these parasites. Thus, the present writer (Van Cleave, 1925: 150) called attention to the fact that Amphibia of Japan harbor species of Acanthocephala specifically different from, yet showing tangible relationships with, the parasites of European Amphibia. The only plausible explanation of such an instance of parallel evolution evidenced in the relationship of parasite and host seems to rest in the postulate that the relationship between the parasite and the host antedates the existence of present-day species of either the host or the parasite. A form ancestral to present-day species of Amphibia in Europe and in Japan, doubtless harbored acanthocephalans from which the parasites of these two faunas evolved, while the host faunas themselves were being differentiated. Such observations, which in volume might be extended beyond the single cited example, provide the only evidence of the existence of Acanthocephala prior to the present geological period. There are no records in the literature of any fossil forms which show incontestable relationship with present-day Acanthocephala. As pointed out later in this review, Meyer has considered certain fossil forms, which are generally classed with the Gephyrea, as strikingly resembling the Acanthocephala in their general body form. An agreement of this sort is based on the same superficial resemblance which led zoologists to assume round-worm relationships for the Acanthocephala. Members of a group which have been obligatory parasites for such

a long time that all free-living stages have been eliminated from the life cycle and all organs characteristic of free life, even including the digestive system, have wholly disappeared could scarcely be expected to show many points of fundamental similarity to organisms which lead an independent existence. With the evidence from paleontology almost wholly wanting, the fields of taxonomy, comparative anatomy and ontogeny must be relied upon to furnish the main body of evidence regarding the relationships of the Acanthocephala. The tangible evidences, though fragmentary, will be presented in the following section.

Any discussion of phylogeny of the Acanthocephala can not fail to give prominence to that most significant distinction, the complete lack of digestive organs and the absence of any recognizable vestiges throughout life. Such a state points to a long established condition introduced so early in racial history that even vestigial remains have failed in transmission through larval stages down to present-day forms. The universal association of lack of specialized digestive organs with the parasitic habit immediately suggests the possibility that adaptation to parasitic mode of life may extend back through the line of descent of the Acanthocephala into the remote ancestral stem from which the present-day group has evolved. A survey of the worm groups in which parasitism has become fixed as an obligatory mode of life reveals but one group that can provide the background of antecedents from which the gutless Acanthocephala could emerge. Aside from the Acanthocephala, the Cestoda comprise the only other group of parasitic worms which lack all vestiges of the digestive organs. This fact in itself might be taken as indicative of a possible common ancestry, but the proof of relationship could not rest on the occurrence of a negative character which might have arisen independently in the groups; further and positive direct evidence of kinship must be sought in the details of morphology and ontogeny possessed in common by the two groups.

Cholodkovsky and other writers have expressed the belief that the cuticula ensheathing the body of all acanthocephalans more closely simulates that of the cestodes than that found in the nematodes. On the whole, the structure of the subcuticula and of the body musculature much more closely correspond to similar cestode tissues than to those of nematodes. In the genera *Arhythmorhynchus*, *Polymorphus* and *Centrorhynchus*, the subcuticula of the anterior region of the body shows very distinct tendencies toward the formation of a parenchyma. The differentiation of the body musculature into circular and longitudinal layers is distinctly in favor of flatworm relationship.

Chitinized structures such as the proboscis hooks and body spines give evidence of a much closer agreement with cestode than with nematode conditions. While there is great diversity in form of proboscis hooks in the Acanthocephala, several types show profound similarity to the rostellar hooks of the Taenioid cestodes and others with the hooks covering the proboscides of the Trypanorhyncha. The large proboscis hooks of *Hamanniella* as figured by Travassos (1917; pl. 6, fig. 33) are identical in detail of form with the hooks of *Taenia taeniaformis* as figured by Hall (1919, p. 9, fig. 3). Similar citations could be made showing close agreement in hook form between numerous acanthocephalan and cestode genera, but since no claim is made for direct relationships between the genera compared, further examples will not be listed.

Superficially, the lacunar system of an acanthocephalan resembles the vascular system of a tapeworm strobila with its longitudinal and transverse vessels. Homologies are not claimed for these structures. No recognizable counterparts are found in the Nematoda.

As high distinctive organs of the Acanthocephala, the lemnisci should be mentioned in discussing the origin of this group. Though their functions are very imperfectly understood, the lemnisci stand without recognized

counterpart in other groups of the animal kingdom. Hamann (1891) has shown that they arise late during ontogeny; thus, as coenogenetic organs they have little value in determining the phylogeny of the Acanthocephala. Both by origin and by association, they represent a definite association with the subcuticular tissue of the body. They are vestigial structures or embryonic rudiments of ectodermal tissue which have failed to proceed with differentiation.

Though specialized excretory organs are wanting in most of the Acanthocephala, protonephridial organs have been described for a number of genera of the Archiacanthocephala. This point in common between Acanthocephala and Plathelminthes seems so very obvious that the history of interpretation of these organs should be traced. The earliest observers of these organs, which are associated with the genital system, did not understand their excretory function (Leuckart, 1876; Andres, 1878). Through his morphological and physiological studies, Kaiser (1892, 1893) interpreted their excretory function and though he saw likenesses between these organs and the flame-cells of flatworms he thought of these likenesses as superficial and considered the nephridia of *Macracanthorhynchus* as without direct parallel in other worm groups. Because of the shape of the nephridia in this genus, Kaiser thought them more easily derivable from nephrostomes of annelids than from protonephridia of flatworms.

Meyer (1930) and others have added materially to the knowledge of excretory organs in the Acanthocephala since the time of Kaiser. Meyer described a type of protonephridial organ for *Oligacanthorhynchus* different from the irregularly branching organs of *Macracanthorhynchus*. In this second type, large numbers of protonephridial units are arranged radially around a central nephridial chamber. Following the earlier position of Kaiser, Meyer evaluates these as more closely resembling the segmental organs or metanephridia.

In recent years the discovery of diverse plans of organization of protonephridial organs in the flatworms throws doubt on the significance of the differences between these organs as they appear in the flatworms and the Acanthocephala. At least it is evident that the tufts of cilia in the excretory tubules of Acanthocephala point to a possible common relationship with flatworms, while denying any possible relationship with the Nematoda.

Through the organs of reproduction are revealed some of the closest parallels with conditions in the Cestoda. The condition of separate sexes, which might be considered as more closely resembling Nematoda than Cestoda, while not frequent in cestodes does occur with sufficient frequency to emphasize the potentiality of separation of the sexes resident in the ancestors of the cestodes. In both sexes, the gonads of Acanthocephala present distinctive cestode conditions.

The reproductive organs of the male acanthocephalan show many points of agreement with those of the cestodes and no essential similarity to the continuous filiform gonad and duct of the nematodes. Intromittent spicules, characteristic of male nematodes, are never found in the Acanthocephala, where the cirrus is invariably a fleshy, retractible organ somewhat like that of cestodes. The persistent gonad of female nematodes continuing as a tubule but slightly modified into regions for the fertilization and storage of the eggs stands in sharp contrast with the temporary ovary of the acanthocephalan female and the highly complicated genital tract. The writer is unable to point out homologies between the female genital organs of Acanthocephala and of Cestoda in the convincing detail employed by T. Odhner in his article (1912) establishing homologies between the organs of cestodes and trematodes.

One line of argument for common origin of cestode and acanthocephalan branches that has never before been emphasized is that of common tendency toward introvert formation. In the cestodes the cirrus of the male, the

rostellum, and particularly in the Trypanorhyncha the four proboscides are structures which are in most instances capable of being retracted within receptacles. Significantly similar introverts are found in the proboscides of all the Acanthocephala. The cirrus of the male acanthocephalan does not undergo inversion when it is withdrawn into the body, but the whole posterior region of the body, the bursa, associated with the cirrus behaves much like an introvert. The copulatory bursa is retractible within the posterior region of the body instead of remaining a permanently extruded external organ as in the nematodes. The writer does not claim to have established rigidly construed homologies between the rostellum and proboscides of cestodes and the acanthocephalan proboscis, for knowledge of the details of the embryonic history is too fragmentary but in morphological relations, the hook-covered hold-fast organs show such uniformity of characters as would be expected in groups arising from a common source.

Between the proboscis of the Acanthocephala and the male genitalia of the cestodes there exists a similarity in organization that may be only accidental, but which has appealed to the writer as possibly reflecting a potentiality in the direction of differentiation of greater significance than mere chance parallelism. The proboscis and its receptacle with the associated musculature permit of intimate comparison with the cirrus, cirrus sac and musculature of the male genitalia of the Cestoda. The similarity is heightened by the frequency with which the cestode cirrus is spine-clothed. It may be fanciful, but at least it provokes thought when a comparison is drawn between an individual acanthocephalan body and an isolated proglottid of one of the cestodes provided with two sets of genitalia. In such a fanciful comparison, one set of genital organs remains functional at one extremity of the isolated proglottid and the set at the opposite extremity might become modified as an attachment organ. One spine-covered cirrus represents the pro-

bosic; the cirrus sac, the receptacle; degenerated gonads and associated structures might become the genital ligament ensheathing the remaining gonads and accessory glands. In enumerating such possible correlations, no claim or proof of homology is advanced. It seems sufficient to point to the possible basic resemblances of diverse structures as indicative of harmonious pattern where proofs are lost in an unrecallably remote past.

The assumption that the body of an acanthocephalan is normally circular in cross-section is probably responsible, more than any other single point, for general adherence to the belief that the Acanthocephala are "roundworms." In fact, the bodies of many species are distinctly flattened as they lie in the lumen of the intestine of the host. The plump, rounded bodies so familiar to the student of preserved collections, are not characteristic of the living worms. Osmotic changes, incident to transfer of the worms to water or to the killing solution, are responsible for the turgidity which distends the body into its rounded contours. The "roundworm" form is thus an artifact not characteristic of the living Acanthocephala.

It is interesting to note that some of the very earliest references to Acanthocephala were made by students observing the living worms in their flattened state. Meyer (1932: 4) attributes the first recognizable description of any acanthocephalan to Anton van Leeuwenhoek, in 1695. Describing specimens from an eel, he mentioned the fact that the body was flattened. It is not surprising that with the scanty morphological knowledge at their disposal many of the seventeenth and eighteenth century observers were misled by the flattened body to commit the common and frequent error of calling thorny-headed worms "Taenia" or "Fasciola." On the other hand it is somewhat of a reflection on the original observations of later investigators who were evidently more familiar with bloated, preserved worms than with the living parasites and therefore saw only "round-

worm" features. An aura of prophetic utterance may surround the errors of earlier investigators. Some might see in Pallas' erroneous assignment of Acanthocephala to the genus *Taenia* a prophetic understanding of flatworm relationships of the Acanthocephala. But details in support of such assignment were wholly lacking in the eighteenth century even though they have been provided more recently. "Lucky" errors are not to be confused with supernatural divining powers.

Hamann (1891) called attention to the fact that cross-folds on the bodies of certain species of Acanthocephala are due to muscular contraction and have no facts of internal organization giving evidence of metamerism or strobilation. Instead of arguing against an ancestry common with the cestodes, this fact gives support to the flatworm origin of the thorny-headed worms. The continuity of evolution prevents the recognition of present-day species of cestodes as the "ancestors" of the Acanthocephala. Strobilation is not an inseparable attribute even of modern cestodes and much less an imperative postulate for the flatworm stem which gave rise to both cestode and acanthocephalan branches. In fact, strobilation is by no means a character of uniform manifestation in the modern Cestoda. It is lacking in the monozoic cestodes. Ligula, a polyzoic cestode with metamerically disposed sex organs, lacks transverse partitions essential for proglottid formation.

The metameric arrangement of musculature in genera such as *Moniliformis* and the orderly sequence of the circular canals of the lacunar system in forms such as *Mediorhynchus* lay a scene for strobilation just as perfectly as does the metameric gonad arrangement of *Gunda* mark a transition between the unsegmented flatworms and the establishment of segmentation as maintained by students of phylogeny. In seeking relationships of groups having common origin, though long separated, we must not expect to find identity in characters, since progressive or regressive evolution

continues to operate on the branches that arise from a common stem. We should expect harmonious or integrating characters rather than close duplication of details in two groups that have been long established though they might have had common origin.

Anton Meyer (1928:199) draws detailed comparisons between the cleavage stages of *M. hirudinaceus* (*G. gigas*) and of the Rotifera and expresses interest in possibilities of relationship between the Acanthocephala and the Rotifera. The same author (pp. 203 and 214) finds significant agreement in the nature of the shell surrounding the embryonic larva of Acanthocephala and Priapuloida and on this basis points to a plausible relationship between the two groups, supported further by details of female reproductive organs and several other points of similarity. He agrees with H. Hammersten (1915) in separating the Priapuloida from the sipunculids and places them with the Acanthocephala in a group which he names the Aschelminthes. As pointed out elsewhere in this paper, agreement in cleavage pattern can not be taken as indicating anything more than possibility of a common ancestry and has no necessary implication of immediate relationship.

The embryo in Acanthocephala, within the confining membranes, shows many points of structure in common with that of tapeworms. The presence of hooks so frequently cited as diagnostic for cestode embryos is a character also shared by the acanthocephalan embryo. There is lack of full agreement as to the number of embryonic hooks on the acanthocephalan embryo, but so also is there evidence of deviation from the hexacanth condition in the cestode larvae. From six to eight spines have been given as the number of embryonic spines in the larval Acanthocephala (Hamann 1891:9), though Leuckart records ten for *Pomphorhynchus*. Similarly, in Lankester's "Treatise on Zoology" (Part 4, page 103), the embryos of *Amphilinea* and of *Gyrocotyle* are said to have ten spines. Thus variations

from the typical hexacanth condition are just as pronounced in cestodes as in the group of Acanthocephala. In more than superficial manner does the shelled embryo of an acanthocephalan furnish points for direct comparison with the shelled embryo of cestodes. Though embryos of cestodes characteristically have spheroidal or ovoidal form some species have elongate embryos closely resembling the spindle-shaped embryos of some Acanthocephala.

In general plan and in rather intimate details, the life cycle characteristic for the Acanthocephala closely resembles that of the more primitive cestodes. So far as is known, all acanthocephalan life cycles involve two hosts, one a vertebrate sheltering the mature worms in its intestines, and the other an arthropod in whose viscera organogeny proceeds. The arthropod devours the shelled embryo as in the life cycle of many of the tapeworms. The chief difference here lies in the fact that the acanthocephalan represents the extreme of adaptation to parasitic existence, for the embryo never hatches normally outside the body of the arthropod host while a free larval period is not uncommon among the cestodes. The acanthor which is liberated from the acanthocephalan embryonic membranes seems to be more highly specialized than the hexacanth larva of the cestodes, for the former is an obligatory parasite throughout its existence, while at least potentially the cestode larva may engage in a period of free life with functional cilia as specialized organs of locomotion.

While the evidences cited in the present review are from morphological studies, there is a growing literature on experimental work throwing some light on acanthocephalan relationships. As a single example, Eisenbrandt (1936:324) in comparing precipitin tests of various helminthes found that the antigens from two species of tapeworms gave reactions "which indicate a relationship between the Acanthocephala and the Cestoda rather than the Nematoda."

In the preceding paragraphs it has been shown that in fairly intimate detail of structure, life cycle and relationships to the hosts, Acanthocephala have numerous points in harmony with conditions found in the Cestoda. The writer realizes that in many details the likenesses between Acanthocephala and Cestoda are so sketchy that they are best viewed with squinted eyes. But he has not aimed at establishing identity of the two groups. Points which show general agreement often lack in specific detail and yet are available as plausible evidence for common ancestry. The most significant points of difference will be summarized briefly and left without further comment.

The acanthocephalan body cavity is without parallel in the Cestoda. The form of the protonephridial organs in Acanthocephala is fundamentally different from that encountered in the flatworms yet both are protonephridial systems. The proboscides of the Trypanorhyncha though in form superficially resembling the acanthocephalan proboscis are fundamentally different in internal structure as well as in method of operation. The body musculature, though showing agreement in layering is strikingly different in cytological details in the two groups. In enumerating these samples of incomplete harmony between Cestoda and Acanthocephala, it may be suggested that they represent advances and divergences within and between the two groups in the period since they broke off from a common line of descent to form two relatively independent groups, each of which has gone its own way of specialization, retaining here and there threads of likeness, not complete identity.

In conclusion, a review of the evidence gives ample proof that the Acanthocephala have little in common with the Nematoda. The grouping of Acanthocephala with any of the various aggregation of animals that have been proposed lacks convincing evidence of natural grouping based on common origin. Only with the Cestoda are impelling evidences of relationship traceable,

but these are of a degree denoting long separation. It seems clear that recognition of Acanthocephala as an independent phylum best measures the extent of isolation of this group. In allocating this phylum it should be placed immediately adjacent to the Plathelminthes in recognition of the many points held in common by Acanthocephala and Cestoda.

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HYBRID VIGOR AND ITS UTILIZATION IN SWEET CORN BREEDING¹

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At the same time Gregor Mendel was carrying on his experiments with peas, Charles Darwin was studying the effects of self and cross fertilization in the vegetable kingdom. The results of several years' research were published in 1876. Working with many species of plants, including *Zea mays*, Darwin found that on the whole the crossed plants were taller than plants selfed one generation or more. In maize the height ratio of crossed to selfed plants was 100:84. Darwin's work had its effect on maize breeding in the United States. In 1862 William James Beal went to Harvard to study natural science with Asa Gray, a supporter of Darwin. Beal undoubtedly learned of Darwin's researches on cross and self fertilization, since Gray and Darwin corresponded frequently.

Not long after Beal went to the Michigan Agricultural College in 1870, he planned an experiment to test the grain yield of crossed and open pollinated varieties of maize. In 1881 he grew the first crossing plot in which one variety was detasseled and pollinated by the other. In three different years the crossed plants out-yielded the open pollinated parents. Apparently the increased yields were not sufficient to create any interest in hybrid corn.

Hybrid corn as we know it to-day owes its origin to an experiment in theoretical genetics. In the autumn of 1904 Dr. George H. Shull began counting row numbers on some white dent corn that had been grown for livestock feed at the Carnegie Station for Experimental Evolution in Cold Spring Harbor, Long Island, New York.

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He was interested in the inheritance of row number, but up to this time had not been particularly interested in the maize plant.

In the summer of 1905 he made his first self-pollinations to study what effect selfing a normally cross-breeding plant would have on the inheritance of a "fluctuating" character. He found a marked reduction in vigor upon inbreeding with the subsequent increase in vigor when different lines were crossed. With comparatively few data Shull immediately made an accurate analysis of what was happening. He discovered that the inbreeding was separating the heterogonous maize plant into a number of pure lines, or biotypes. The pure lines when crossed not only gave a vigorous hybrid, but produced for the first time a maize variety whose heredity could be rigidly controlled.

Here Shull's experiments opened a new era in maize breeding. Controlled heredity is the factor that has made hybrid corn so superior to open-pollinated varieties. Before Shull all the progress in corn breeding had been made by the use of mass selection, and with considerable success by many practical corn breeders. Shull proposed an entirely different attack—a method of first isolating pure lines, and then crossing them to give a uniform, more dependable result. His two classic papers "The Composition of a Field of Maize" and "A Pure Line Method in Corn Breeding" outline the method in use to-day, thirty years later.

In presenting this brief historical sketch of hybrid corn, the work of Dr. E. M. East must be mentioned. According to popular belief, Shull and East conducted their experiments independently, and came to the same general conclusions. This statement is not entirely true, although it can be found in several publications, including one of our own. In preparing this discussion all the original papers have been consulted as well as certain correspondence between East and Shull. Accordingly, a more accurate picture of the early developments in in-

breeding and crossing maize has been obtained, we believe, than any previously published. For this reason, let us take time to get the record straight.

East began selling corn in 1904 in Illinois to study the effect of inbreeding. After Shull's paper East realized his results were similar to those of Shull and wrote considerably on the subject of corn breeding. His writings undoubtedly stimulated other workers. East, however, stated that he believed the pure line method of Shull to be impractical, and as late as 1912 recommended crossing of varieties as the most practical means of utilizing hybrid vigor. It remained for many workers in the state Agricultural Experiment Stations, the United States Department of Agriculture, seedsmen and farmers to prove the practical value of the new method of seed production.

The pure line method of Shull has found its most rapid fulfilment in sweet corn breeding. Considerably more than 75 per cent. of the sweet corn produced commercially in the United States to-day is hybrid. (Approximately one-half million acres of sweet corn are grown each year.)

The first hybrid sweet corn was a sun red, white seeded Evergreen, called Redgreen, introduced by D. F. Jones in 1924. This hybrid is a single cross, the F_1 hybrid of two inbred lines, Connecticut 75 and 77. Redgreen is a late hybrid, has excellent quality, and is grown largely for canning.

Hybrid sweet corn made little progress generally until the introduction of Golden Cross Bantam in 1932. This is a hybrid between Purdue 39, an inbred of unknown parentage, and Purdue 51, a Golden Bantam inbred. Golden Cross Bantam was produced by Dr. Glenn M. Smith, of Purdue University and the United States Department of Agriculture. It is remarkably productive, has a good-sized ear of excellent quality, is uniform in time of maturity, and is resistant to bacterial wilt, a disease that decimated some of the open-pollinated varieties a few years ago. Golden Cross Bantam was introduced at a time when there was a severe epidemic of bacterial

wilt. Its ability to produce a crop of good-quality ears under adverse environmental conditions not only created for itself a place in our permanent agriculture, but established the pure line method beyond any possible question. Its success was rapid. In 1935, three years after introduction, more than one million pounds of hybrid seed were produced and it has been in the million-pound class ever since, a remarkable record.

Too much time would be consumed should we attempt to enumerate all the other successful hybrids that have appeared in recent years. The most important ones produced by the Connecticut Experiment Station are Spancross (C4.13), Marcross (C6.13) and Carmelcross (P39.C13). The inbred Connecticut 13 is extremely early, is almost immune to bacterial wilt and combines well with other inbreds to give productive hybrids. It was secured from Goden Early Market, a distinctly susceptible variety.

The most successful sweet corn hybrids are single crosses, the cross of two inbred lines, while a few are top-crosses, the use of an inbred pollinator on a commercial variety. This method, proposed in 1931 by Dr. E. W. Lindstrom, has found its greater use in sweet corn breeding. With better inbreds increasing, the trend is toward single crosses. In regard to uniformity the single cross has an advantage not possessed by the other types of hybrids. Sweet corn is largely grown by market gardeners who supply green corn to the market, or by canners. Both want to harvest their crop at one or two pickings, which is possible with the single cross.

In field corn, modification of Shull's pure line method was necessary to make it practical. This was largely because the inbreds are unproductive, and also because the smaller seed of the inbreds does not work well in the corn planters adapted to the larger varietal seed.

This modification was made by one of East's students who had become interested in hybrid corn largely through East's writings. Here again was a major contribution,

as in the case of Shull, by a man who had little experience with corn. Dr. Donald F. Jones, a native of Kansas and originally a horticulturist, was assistant in plant breeding at the Arizona Experiment Station when he became interested in genetics. He went to study with East at Harvard in 1914, and the next year became geneticist at the Connecticut Experiment Station in New Haven. Possibly because he had little experience with corn, he was interested in the idea of crossing pure lines, when he came to New Haven. He spent his first summer at New Haven, 1915, increasing the inbreds.

The next year, Jones had a crossing plot of inbreds, some of the same ones started by East. That summer, while watching the growth of the weakened inbreds, he planned the double cross. In 1917 he grew a crossing plot using first generation hybrids for parental stocks. The following year many double crosses were tested for yield. One was markedly superior to the other hybrids and open-pollinated varieties. This hybrid was re-tested in the following years and in 1921 was released as Double Crossed Burr-Leaming.

In this session we can trace only in outline hybrid corn from its inception to its fulfilment. Naturally, the researches of many workers have been omitted. We wonder if it is a coincidence that the two men making the greatest contribution to this work, Shull and Jones, were primarily not corn breeders. One was a botanist, the other a horticulturist. Is it possible that beginning research with minds unclouded by previous experience in maize breeding, they were more willing to try new methods to find solution of their problems?

How the genes in maize operate to produce a hybrid superior to the parents, has not been fully explained. Many scholars and men of science have been fascinated by the phenomenon of hybrid vigor. The work of Darwin and Beal has already been mentioned. Dr. Samuel W. Johnson, first director of the Connecticut Agricultural Experiment Station and professor of chemistry at Yale

University, in the 1891 edition of his book "How Crops Grow" said, "That crossing commonly gives better offspring than in-and-in breeding is due to the fact that in the latter both parents are likely to possess by inheritance the same imperfections, which are thus intensified in the progeny, while in cross-breeding the parents more usually have different imperfections which often, more or less, compensate each other in the immediate descendants." In the light of later knowledge, we realize this is a keen observation. It shows the Darwinian influence since there is no mention of this in the previous edition (1868).

The explanation of Shull and of East was that the increased growth was due to a physiological stimulus of heterozygosis. Jones in 1917 proposed "The Dominance of Linked Genes Hypothesis," giving hybrid vigor a genic or factorial interpretation. According to this theory the increased growth of the F_1 plants is due to a dominant action of different dominant growth factors contributed by each inbred parent. The use of dominant growth factors, without linkage, had previously been suggested by Bruce (1910) and by Keeble and Pellew (1910). The introduction of linkage into the picture by Jones was considered necessary to overcome two objections to the theory without linkage. One objection is that in an F_2 segregation there would be a skew distribution if dominant un-linked factors are segregating. Such a condition does not exist, as was shown by Emerson and East (1913) in their comprehensive researches on the inheritance of quantitative characters in maize. With a large number of factors, however, the skewness would not be observed in ordinary sized populations. The segregates would all fall in the classes for the large factor numbers and would approximate a normal curve as was pointed out by Collins (1921).

The second objection was that without linkage it should be possible to combine all the favorable growth factors in one individual and obtain a homozygous, true breeding,

vigorous line. This objection is not crucial. Collins has pointed out that linkage is not necessary to prevent obtaining a homozygous individual with all favorable factors present in a homozygous condition. With a small number of factors this would be true. With a large number, however, it would be virtually impossible even without linkage.

Thirty factors, three to each chromosome, is the maximum allowed by the present map distances without having considerable linkage between factors on the same chromosome. For the sake of argument let us suppose the map distances will be extended so that there could be thirty factors in maize showing no linkage whatever. Let us see how much land would be required to grow enough plants to obtain an individual homozygous for all thirty factors. (With linkage more space would be required.) With thirty factors it would take an enormous number of plants (4^{30}) to have an even chance of obtaining a homozygous plant containing all 30 factors, even if we could tell such a plant when we found it. To grow this number of plants (at the normal spacing) would require a land area more than 2,000 times the total land area of the earth. So we see the possibilities for obtaining such an individual are quite rare. With more factors, and with linkage which would accompany the increased factors, we see how futile are the attempts to obtain an inbred with any great number of homozygous dominant growth factors.

Jones's theory has been quite generally accepted by the maize geneticists, although as yet there is little critical evidence to differentiate this from the stimulus of heterozygosis. Richey and Sprague planned an experiment to test this point. In their convergent improvement studies, an F_1 hybrid was backcrossed to each of the two parents in two separate backcrossing programs. While backcrossing, an attempt was made to select characters of the other parent and thus converge into one line the good characters of the two inbreds. After several generations

of backcrossing the converged lines were crossed with the non-recurrent parent. The new lines should be more similar to the non-recurrent parents, since they now contain some of their germ plasm. Hence, if hybrid vigor is due to a stimulus of bringing together diverse germ plasms we would not expect as much vigor from using one of the converged lines as from crossing the two original ones.

The small amount of experimental evidence available on this point, obtained by Richey and Sprague, suggests that the yields of the new F_1 hybrids may be as great as the F_1 hybrid from original lines. Six crosses were tested for yield, comparing the original F_1 hybrid with the new hybrid, made by crossing one of the original inbreds with a new converged line representing the other inbred parent. Of the six hybrids tested, one comprising the converged inbred yielded the same as the original F_1 hybrid, two yielded less, and three yielded slightly more. The differences in all cases were small and barely significant statistically. These experiments need further corroboration before it can be stated that inbreds can be secured from such a backcrossing program that will, when crossed together, produce better yielding hybrids than the original. In all cases the yields of the inbreds themselves were improved, but the hybrid yields are not convincing.

If there is complete dominance of the growth factors it would never be possible to increase the hybrid yield by crossing converged lines with the non-recurrent parent. This would be true even if *all* of the growth genes in the F_1 hybrid could be made homozygous in a single line. If it can be demonstrated that such a backcrossing program will produce inbreds capable of a higher yield when crossed together than the original F_1 hybrid, then we must assume dominance is not complete. There is no evidence on the completeness of dominance of heterotic growth factors. With the recessive plant character golden, *Gg* plants yield as much as those homozygous for *GG*.

Richey and Sprague have demonstrated that inbreds can be improved by first outcrossing to some other line and then backcrossing several generations to one parent. Such a practice is commonly used by maize breeders throughout the United States. This in itself shows that favorable growth factors are transferred from one stock to the other. This, coupled with the fact that the F_1 -converged-hybrid yields were approximately the same as the original, is evidence in favor of the dominant growth factor hypothesis since the new inbreds are more similar in their germ plasm and should provide less of a physiological stimulus than the original cross.

The dominance of linked growth factors supplied for the first time a factorial interpretation of hybrid vigor. Along with this interpretation came the general realization that a large amount of material must be used in an inbreeding program if really superior germ plasm is to be obtained. This was emphasized by Jones in 1920. Shull had previously found that different inbreds gave different degrees of hybrid vigor when crossed, and advocated extensive research by the Experiment Stations to find the best yielding combinations.

Dobzhansky and Rhoades (1938) proposed the inversion method for locating favorable growth genes by crossing an inbred stock to homozygous inversions on each of the ten chromosomes. We will use their illustration for Chromosome 1. A homozygous inversion is produced by x-rays in an inbred stock. This stock, also PP (the pericarp factor), is crossed by an inbred that is p . The F_1 hybrid is either selfed, or backcrossed to the inbred p . Two stocks will be obtained, one pp having the Chromosome 1 pair from the inbred tested, the other Pp having one pair of chromosomes from the inversion stock. Any excess in yield of Pp over pp will be due to favorable growth genes located in Chromosome 1 of the inversion used. By comparing different inbreds it will be possible to see which ones contain less favorable factors in Chromosome 1. If inbred A under such a test yields ten

bushels less than the *Pp* stock, while inbred B yields only five bushels less, it will be safe to assume that inbred A carries fewer good growth factors in Chromosome 1.

The value of this method will need to be tested experimentally. One possible question occurs to us. Will the differences between the two lines compared, after one generation of backcrossing, be large enough to be convincing, or will they be masked by the heterozygous genetic constitution of the other nine pairs of chromosomes? Perhaps it would be better to backcross several generations to the *p* inbred tested, keeping the *Pp* factor, and consequently the inversion heterozygous, and in the end secure two stocks that are virtually homozygous for nine chromosomes. The only difference between the two stocks would be located in Chromosome 1. At this point it would be better to cross the two stocks by another inbred or variety, and study the difference in yield between hybrids produced using the two different inbred stocks. This latter procedure is necessary because the growth and yield of an inbred itself is no criterion of the growth factors it transmits to its hybrids. We are interested primarily in the growth factors an inbred transmits and not merely in factors that make it a good inbred.

We wish to propose the multiple recessive method for locating favorable transmissible growth genes in maize inbreds. By this method the inbred is crossed by multiple recessive characters on each of the ten chromosomes. Let us use as an illustration Chromosome 2 with the recessive characters *lg gl₂ b v₄*, which we shall cross by C75, a sun-red inbred dominant for the factors used. The *F*₁ will be selfed (this can be done in the greenhouse in the winter crop) and the next year the recessive will again be crossed by the dominant. After three or four backcrosses two stocks will be obtained $\frac{lg\ gl_2\ b\ v_4}{lg\ gl_2\ b\ v_4}$ and the dominant *Lg Gl₂ B V₄* which may be homozygous or heterozygous for these characters. This can be made homozygous and both homozygous dominant and homozygous recessive.

sive stocks crossed with Purdue 39. A yield comparison can be made between $\frac{lg\ gl_2\ b\ v_4}{P39}$ and $\frac{Lg\ Gl_2\ B\ V_4}{P39}$. Any excess of the latter over the former should be due to the favorable growth factors of C75 located in Chromosome 2. All of the ten chromosomes can be tested in this manner. It may be useful in this experiment to incorporate a small-pollen gene to serve as a dominant marker and possibly reduce crossing over, as it does on Chromosome 10 (Rhoades and Rhoades 1939). Small-pollen genes are now available on Chromosomes 4, 9, and 10, and others will undoubtedly be located.

In closing let us briefly summarize our present knowledge of hybrid vigor, and also set down points upon which more evidence is needed. The utilization of hybrid vigor in producing sweet and field corn hybrids has far exceeded our knowledge regarding the working of this vigor. In any inbreeding program it is known to be advantageous to select for many morphological characters that follow definite laws of inheritance. Some of these characters are: good root system, stiff stalk, few or many tillers, good grain quality, resistance to heat, drought, cold, various insects and plant diseases such as smut, rust, bacterial wilt and stalk and ear rots. Inbreds can be secured that will transmit these characters to their offspring. It is along these lines of selection that most of the progress in maize breeding has taken place.

What about selection for the factors responsible for hybrid vigor? Here no criterion of selection is available. The only way to determine the merit of an inbred is to test it by crossing. This crossing is now done at a much earlier generation than formerly. Jenkins (1935) has shown it is possible to cross lines inbred only two generations and select the high yielding ones. Jones and Singleton (1935) have corroborated this finding. Also some of our unpublished data indicate this crossing can be profitably done after one generation of selfing or even in the open-pollinated ear lines before selfing. These results

are a little difficult to explain. They can be interpreted to mean that there are very great differences in the number of dominant growth genes possessed by the progenitors of the inbred lines, and that these differences in numbers establish the differences that the inbred lines later show. We can not say whether this is the correct interpretation.

One very puzzling thing about hybrid vigor is why the dominant growth factors do not make themselves manifest more in the inbreds. Why do not these genes governing heterosis make more of a difference on the inbred parent? It is common knowledge that some vigorous inbreds give little response upon crossing while other weaker lines give a large response. There is a small positive correlation between good growth in inbreds and hybrids. The genes responsible for heterosis must be different from the normal growth-promoting genes of a plant. Perhaps the genes responsible for heterosis act more in the nature of complimentary factors similar to the color genes A, C, and R that give a colored aleurone when all three are present, yet give colorless aleurone when any one is lacking. If this were the case it would explain why the heterotic factors have so little effect on the inbreds.

We look to future researches to locate on the chromosomes some of the heterotic genes, and for more definite knowledge regarding the workings of such genes. Probably no single interpretation so far advanced will completely explain hybrid vigor. We hope the next thirty years will be as productive in untangling the riddle of heterosis as the past thirty have been in making practical application of it.

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CHEMICAL FACTORS DETERMINING THE CHOICE OF FOOD PLANTS BY PAPILIO LARVAE¹

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It is becoming increasingly apparent that phytophagous insects are not so catholic in their food preferences as was formerly believed. Even insects that subsist upon a variety of plants exhibit definite predilections. The problems associated with the selection of food plants involve many varied though none the less related phases. There is no escaping the fact that the choice of food is largely predetermined by the gravid female at the time she selects the place to lay her eggs. Just what factors are here involved lies beyond the scope of these studies. Simple experiment and casual observation show that larvae are capable of recognizing certain specific plants and can, therefore, exercise a choice. Whether or not the insect is able to ingest or digest the plant it has chosen, or whether it can live, grow and reproduce on this host plant is a matter of nutrition. The present investigations are concerned with the primary factors operating in the selection of food plants by *Papilio* larvae. These factors, be they repellent or attractant in nature, determine the susceptibility or immunity of a plant to attack by insects. Repellent factors are very frequently physical in nature as exemplified by a leaf of extreme toughness or by pubescence. They may also be chemical. Attractant factors are entirely chemical.

Odor is the most important property of a plant by which a phytophagous insect recognizes it as a food plant. This was indicated by the following experiments (Dethier, 1937); First, larvae of *Danaus plexippus* L., separated from *Asclepias*, their food plant, by wire screening, described searching movements when they passed over

¹ This work was aided by a Harvard University fellowship for study at the Atkins Institution of the Arnold Arboretum in (Soledad) Cienfuegos, Cuba.

these leaves but maintained straight paths when passing over other leaves. Second, larvae refused leaves treated with methyl alcohol as long as the odor of the alcohol remained. Subsequently, the leaves were eaten. Third, leaves treated with odorous substances were refused, whereas those treated with salt solutions were repeatedly investigated.

The exact relation between the insect, the odor of its food plant, and plant chemistry was first pointed out by Verschaffelt (1910). Mustard oils (alkyl-isosulphocyanates) and closely related chemicals normally present in Cruciferae as well as in a few other plants, in pure form served as attractants for *Pieris* larvae.

This suggested that other plant odors could be correlated directly with specific chemicals and the insect-chemical relationship be established in additional groups. The results embodied in these studies indicate just such a relationship within the genus *Papilio*.

I

In current literature the larvae of *Papilio ajax* L. are listed as feeding upon various Umbelliferae. It first became necessary to test this statement by feeding to the larvae of this species all members of the Umbelliferae available at the time. As a result it was found that the following umbelliferous plants were all eaten to a varying degree:

Pteroselinum sativum Hoffm.
Cicuta maculata L.
Conium maculatum L.
Sium circutaefolium Schrank.
Daucus Carota L.
Osmorrhiza longistylis (Torr.) DC.
Carum Carvi L.
Pastinaca sativa L.
Anethum graveolens L.
Apium graveolens L.

To this list may be added the following umbelliferous plants reported in the literature:

Cicuta virosa L.
C. bulbifera L.

Hydrocotyle umbellata L.
Foeniculum vulgare Hill.
Angelica atropurpurea L.
Echinophora spinosa L.
Arracac xanthorrhiza Baner.
Oxyopolis filiformis (Walt.) Britton.

The absolute refusal of many of the larvae to eat *Hydrocotyle americana* (this has been reported at least once as a food plant) suggests that all species of Umbelliferae may not be acceptable. It is of utmost importance that this gap in our knowledge be filled. Under the circumstances, however, it is necessary to base tentative hypotheses upon the characters of the species known to serve as food plants.

The Umbelliferae are characterized by a variety of odors which are said to have a family resemblance. That odors may possess a family resemblance and at the same time retain their specificity is a recognized fact (Delange, 1930; Dumont, 1928). To the human sense of smell the common odors of the Umbelliferae are seven, namely, carrot, caraway, anise, coriander, celery, ferula and angelica. Because of the gaps in our present knowledge it is not yet possible to consider other of the less common odors in this plant family.

As is the usual case among plants these odors originate with the essential oils. The substance giving rise to the odor of carrot is not known. Caraway odor arises from carvone; anise odor from methyl chavicol, anethole, anise ketone and anise aldehyde; coriander odor from cori-

TABLE I
 DISTRIBUTION OF IMPORTANT ESSENTIAL OILS IN THE UMBELLIFERAE

Methyl chavicol	Anethole	Carvone	Coriandrol	Sedanolid
<i>Anthriscus</i> <i>Cerefolium</i> Hoffm. <i>Foeniculum</i> <i>piperitum</i> Sweet. <i>Pimpinella</i> <i>Anisum</i> L.	<i>Osmorrhiza longi-</i> <i>stylis</i> (Torr.) DC. <i>Foeniculum vulgare</i> Hill. <i>F. piperitum</i> Sweet. <i>Anthriscus Cere-</i> <i>folium</i> Hoffm. <i>Myrhis odorata</i> Scop. <i>Pimpinella Anisum</i> L. <i>Anethum</i>	<i>Carum</i> <i>Carvi</i> L. <i>Anethum</i> <i>graveolens</i> L. <i>Pseudocdanum</i> <i>graveolens</i> Benth. & Hook.	<i>Coriandrum</i> <i>sativum</i>	<i>Apium graveo-</i> <i>lens</i> L. <i>Selinum</i>

androl; celery odor from sedanolid; ferula odor from disulphides, especially $C_{11}H_{20}S_2$ (Table I). On the basis of the current food-plant list for *Papilio ajax*, ferula odor may be omitted from further discussions. The question then arises as to whether *P. ajax* is attracted by six different odors or confuses the six as one. There is reason to believe, as will be pointed out below, that the odors are not confused.

The oils, and in some cases the chemicals, from which arise the odors of carrot, caraway, anise, coriander and celery, were procured in pure form.² Although the odor of a plant is the result of a mixture and blending of incredibly minute quantities of many chemicals, there is usually one chemical fundamentally responsible for the odor. The odor of this chemical resembles that of the plant sufficiently closely in most cases to attract the insect; therefore, pieces of filter paper were soaked in the different pure oils, some in methyl chavicol, some in carvone, some in carrot oil, some in coriandrol, and some in celery oil. A necessary precaution is that of allowing the paper to stand for several days before use. Otherwise the oil is of far too great concentration and acts as a repellent rather than an attractant. Experiments are facilitated if the paper is moistened with water, but this is not necessary and if resorted to requires careful control. Although all the *P. ajax* larvae tested attacked the filter paper thus treated, indicating that the oils serve as attractants, most of them did not consume any appreciable amount because of the toughness of the fibers.

On the basis of these experiments it follows that *P. ajax* larvae should be attracted by the same substances when present in other plants provided that the odor due to the attracting compound is not masked by some other more odoriferous constituent. Certain other plants in addition to the Umbelliferae are known to contain carvone, methyl chavicol, anethole, anisic acid, anisic alde-

² With the exception of carvone and methyl-nonyl-ketone, which were put up by the Eastman Kodak Company, all of the chemicals used were put up by the Dodge and Olcott Company.

TABLE II
DISTRIBUTION OF OILS ATTRACTIVE TO P. AJAX IN PLANT FAMILIES OTHER THAN UMBELLIFERAE

Methyl chavicol	Anethole	Anisic Aldehyde	Carvone	Anisic acid
PINACEAE <i>Pinus palustris</i> Mill. <i>P. strobus</i> Mill. <i>P. subnana</i> Dougl. <i>P. jeffreyi</i> Muirt. GRAMINEAE <i>Andropogon nardus</i> Rendl. MAGNOLIACEAE <i>Illicium anisatum</i> Gaertn. <i>I. verum</i> Hook. <i>Magnolia Kobus</i> Kaempf. LABRATAE <i>L. nobilis</i> L. <i>Persea gratissima</i> Gaertn. BURSERACEAE <i>Boswellia serrata</i> Roxb. MYRTACEAE <i>Pimenta acris</i> Wight. LABRATAE <i>Lophanthus anisatus</i> Merr. <i>L. rugosa</i> Fisch. & Mey. <i>Collinsonia anisata</i> L. <i>Ocimum basilicum</i> L. <i>O. sanctum</i> L. <i>O. gratissimum</i> (L.) Boiss. RUTACEAE <i>Boronia serratifolia</i> Willd. <i>Dictamnus Frazinella</i> Pers. <i>Boronia venustum</i> Eckl. & Z. <i>Clausena Anisum-olens</i> (Bl.) Merr. ROSACEAE <i>Prunus lusitanica</i> Lols. COMPOSITAE <i>Solidago odora</i> Alt. <i>S. rugosa</i> Mill. <i>A. remota</i> Michx. <i>A. brenanensis</i> Willd. <i>A. Dracunculidus</i> L. PIPERACEAE <i>Piper Betel</i> L.	MAGNOLIACEAE <i>Illicium anisatum</i> Gaertn. <i>Illicium</i> Hook. <i>Magnolia Kobus</i> Kaempf. LABRATAE <i>Persea gratissima</i> Gaertn. BURSERACEAE <i>Canarium luzonicum</i> Gray. CHENOPODIACEAE <i>Roubleva multifida</i> Moq. PIPERACEAE <i>Piper nigrum</i> L. RUTACEAE <i>Boronia serratifolia</i> Willd. <i>B. venustum</i> Eckl. & Zeyh. <i>Persea madagascariensis</i> Ball. <i>Dictamnus Frazinella</i> Pers. COMPOSITAE <i>Artemisia caudata</i> Michx.	RUTACEAE <i>Boronia venustum</i> Eckl. & Z. <i>Persea madagascariensis</i> Ball. LEGUMINOSAE <i>Acacia Farnesiana</i> Willd. CUCURBITACEAE <i>Cucurbita</i> Hook. ORCHIDACEAE <i>Vanilla planifolia</i> Andr.	PINACEAE <i>Pinus succinifer</i> Clapp. <i>Pinus distichum</i> Rich. <i>Libocedrus decurrens</i> Torr. SCITAMINEAE <i>Cutuma longa</i> L. VERBENACEAE <i>Lippia adoensis</i> Hochst. LABRATAE <i>Libocedrus decurrens</i> Torr. LABRATAE <i>Mentha verticillata</i> var. <i>strabala</i> Briq. <i>M. velutina</i> Lej. <i>M. aquatica</i> L. <i>M. longifolia</i> Huds. <i>M. spicata</i> Huds. <i>Thymus citriodorus</i> L. COMPOSITAE <i>Tagetes minuta</i> L.	LOGANIACEAE <i>Buddleia variabilis</i> Sims. ERICACEAE <i>Betula alba</i> L. RANUNCULACEAE <i>Aconitum Napellus</i> L.

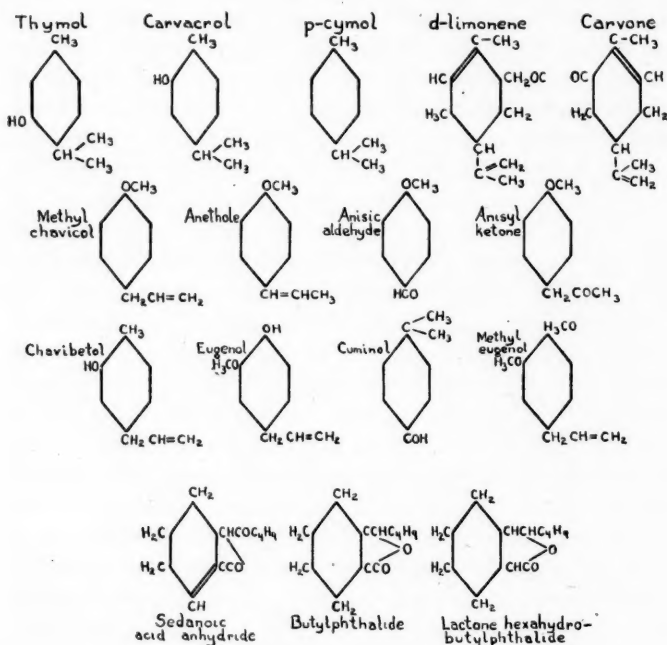
hyde and coriandrol. These are listed in Table II. Theoretically, the larvae should attack the leaves of these species if no masking odor is present. As a matter of fact they do eat *Dictamnus Fraxinella*, *Cosmos*, certain species of *Solidago*, and *Artemisia dracunculoides*, a species closely related to *A. Dracunculus*. Although larvae should be attracted to these plants, it does not follow that they should eat them, for other factors of secondary importance such as leaf thickness, pubescence, etc., come into play and prevent the utilization of the leaf as food.

When one deals with attracting chemicals in pure form, preferences on the part of the larvae become quite obvious. Of all the oils tested above, those with an anise odor proved most attractive to larvae (the caterpillars with which the tests were made had been taken from cultivated carrots). Filter paper treated with methyl chavicol was preferred to fresh carrot leaves. Carrot was preferred to carvone, carvone to oil of coriander. There can be little doubt as to the ability of the larvae to distinguish the different odors. This would seem to indicate, therefore, that an oligophagous species such as *P. ajax* may be conditioned to more than one odor. It would likewise seem that the olfactory sense in these larvae is capable of discriminating among closely related odors. In this respect it simulates the human sense of smell.

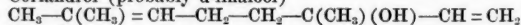
Larvae of *P. ajax* were found in the Gray Botanical Gardens of Harvard University feeding on *Ruta graveolens* L. and *R. patavina* L. The pungent rue odor of these two plants is due to the presence of methyl-nonyl-ketone. Using the same line of reasoning as above it follows that other plants containing this chemical should be attractive to the larvae. The following plants are known to contain methyl-nonyl-ketone: *Citrus Medica* L., *Ruta montana* Mill., *R. graveolens* L., *R. chalepensis* DC., *Zanthoxylum ailanthoides* Sieb. and Zucc., *Z. senagalense* DC., *Empleurum serrulatum* Eckl. and Z., and *Pilocarpus Jaborandi*, all in the family Rutaceae, and *Litsea odorifera* in the family Lauraceae. *P. ajax* larvae have never

been reported from any of these plants. Larvae confronted with *Ptelea trifoliata* L., which smelled faintly like rue, endeavored to eat it but proceeded with difficulty due to the leathery quality of the leaves. *Z. americanum* Mill., which possesses an orange or lemon-like odor plus a very faint suggestion of rue, was also sampled by the larvae which made repeated attacks on the leaves only to be repulsed by their extreme toughness. *Z. simulans* Hance. possesses a carrot-like odor. It is readily attacked by the larvae but is protected by the toughness of its leaves. *Z. schinifolium* Sieb. and Zucc., having a pronounced orange and lemon odor, is not eaten. In *Citrus Medica* L. the odor of rue due to methyl-nonyl-ketone is masked by a pronounced odor of lemon due to the presence of citral. The larvae refused to eat these leaves. Likewise they refused to eat filter paper scented with citral or limonene. Leaves of Rutaceae lacking methyl-nonyl-ketone were not sampled. It is possible that leaves containing it in quantities below threshold value, or leaves containing other constituents in excess, would likewise not be eaten. The attracting quality of methyl-nonyl-ketone is further illustrated by soaking filter paper in the pure compound. This treated paper was readily sampled.

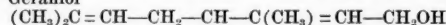
There is no doubt that *P. ajax* larvae are attracted by the odors of carrot (chemical composition unknown), caraway (carvone), coriander (coriandrol), anise (methyl chavicol, anethole, anisic acid, and anisic aldehyde), celery (sedanolid), and rue (methyl-nonyl-ketone). The graphic formulae of these and related compounds are given here. Even a hasty examination reveals that there are certain relationships. Carvone is distinctly chemically related to cymol, thymol, carvacrol (isomeric to thymol), and d-limonene. It is isomeric to limonene which has a distinct lemon odor. The odors of the other three compounds are equally distinct, and the larvae of *P. ajax* are not attracted to them. Methyl chavicol and its isomere anethole upon energetic oxidation yield anisic



Coriandrol (probably d-linalool)



Geraniol



acid and also give rise to anisic aldehyde and anisyl ketone. These five almost identical compounds possessing the odor of anise are related to chavibetol, eugenol (clove odor), methyl eugenol, and cuminal (cumin odor), none of which attracts *P. ajax* larvae. Sedanolide in its various forms is a very different type of compound. Coriandrol (probably identical with d-linalool which does not attract the larvae) and methyl-nonyl-ketone differ from the others mentioned in being chain compounds. Their close relatives have entirely different odors.

This insight into the chemistry of the odors attracting *P. ajax* larvae shows that the larvae do not react to whole groups of related substances but to specific compounds. Apparently the caterpillars are reacting to these com-

pounds because of the odors as we perceive them, and not because of any other property of the compounds. In other words, one appears to be dealing with the same phenomenon in the olfactory sense of caterpillars as in the human olfactory sense. It is hardly necessary to point out that though similar compounds may possess identical odors—as methyl chavicol and anethole (anise odor) and irone, alpha ionone, and beta ionone (violet odor), they may also possess distinctly dissimilar odors—as thymol (thyme odor) and carvone (caraway odor), and benzaldehyde (bitter almond odor) and cinnamic aldehyde (cinnamon odor). On the other hand, decidedly unlike compounds may possess identical odors as exemplified by furfural and benzaldehyde (bitter almond odor).

These preliminary studies also emphasize the fact that mere botanical relationship of one plant to another does not guarantee the use of both by larvae attracted to one.

II

The four hundred or so species in the genus *Papilio* may be grouped into four categories: (1) *Aristolochia*-feeders; (2) species whose feeding habits are varied; (3) *Umbelliferae*-feeders; and (4) *Rutaceae*-feeders. The first two categories have no direct bearing on these studies, but investigations into the feeding habits of the latter two groups shed light upon the apparent trends of evolution of feeding habits in this section of the genus.

Only eleven species of *Papilio* are known to eat *Umbelliferae*. These are *P. ajax* L. and its races, *P. bairdi* Edw. and its races, *P. zelicaon* Luc., *P. indra* Reak., *P. machaon* L. and its races, *P. hospiton* Gen., *P. alexanor* Esp., *P. demoleus* L., *P. ophidecephalus*, *P. constantinus*, and *P. paeon* Boisd. Doubtless the list may be lengthened when our knowledge of the feeding habits of the genus has widened. It seems strange that in a large cosmopolitan group of more or less standard feeding habits a few species should have become rabidly addicted to *Umbelliferae*. A careful study of food-plant lists plus

a consideration of the foregoing experiments suggest a way in which this habit might have become initiated. The fact that Umbelliferae-feeders as exemplified by *P. ajax* will still eat species of *Ruta* suggests that they probably formerly belonged to Rutaceae-feeders.

To understand the transition from Rutaceae to Umbelliferae, it is first necessary to consider the changes that have taken place in Rutaceae-feeders. Rutaceous plants on the basis of their essential oils may be divided into four groups: those with a lemon- or orange-like odor containing citral (*e.g.* *Citrus*), those with a rue odor containing methyl-nonyl-ketone (*e.g.* *Ruta*), those containing both oils in various proportions (*e.g.* *Zanthoxylum*), and those of the mint or camphor type. Most of the evidence points toward species of *Citrus* as being the first host plants of Rutaceae-feeders. The transition from *Citrus*-feeders to *Ruta*-feeders may have been gradual, that is, *Citrus* to *Zanthoxylum* to *Ruta*. Then the transition from Rutaceae-feeders to Umbelliferae-feeders may have been effected by means of *Dictamnus Fraxinella* which contains methyl chavicol and anethole, or *Pelea madagascariensis* which contains anethole. It seems probable, however, that the change to such plants as *D. Fraxinella* and *P. madagascariensis* proceeded by way of intermediates, *Zanthoxylum* and *Ruta*, and not directly from *Citrus*. The proposed line of evolution would then be *Citrus* (and plants containing citral) to *Zanthoxylum* (or other plants containing citral and methyl-nonyl-ketone in varying proportions) to *Ruta* (or plants containing mostly methyl-nonyl-ketone) to *D. Fraxinella* (or similar species) to Umbelliferae. Or *Ruta* may be omitted from the system. *P. cresphontes*, for example, feeds upon: *Citrus*, *Ptelea trifoliata* L., *Zanthoxylum americanum* Mill., *Z. Clava-Herculis* L., *Z. ajuda*, *Dictamnus Fraxinella* Pers., *Nyssa sylvatica* Marsh., *Persea carolinensis* Nees., *Populus pyramidalis* Ait., *Piper peltatum* L., *P. umbellatum* L., *P. aduncum*, and *P. mollicomum* Kunth. In Cuba it also feeds on species of *Triphasia*, *Zanthoxylum coriaceum*

A. Rich, *Atalantia ceylanica* Am. Oliver., *Feronia limonia* Swingle, and *Fortunella crassifolia* Swingle. These plants contain citral and possess an odor of lemon or orange. *Feronia elephantum*, which smelled faintly of rue, was nibbled but slightly. Some species such as *P. andraemon*, *P. cresphontes*, *P. machaon* and *P. ajax* represent various steps in the change from one feeding habit to a new and different one. The acceptance as food of plants from other families (species of *Piper*, for example) may be explained in part by their chemical composition (cf. Table II).

In just what direction *P. hospiton* and *P. alexanor* are headed is difficult to determine in the face of such a paucity of facts. Whether or not they eat any plants other than *Ferula* and *Seseli* is not known. Are they attracted to the characteristic odors of sulphides and thus destined to assay species of *Allium*? Do regular Umbelliferae-eating forms as *P. ajax* feed on *Ferula*?

It is at once apparent that the distribution of both the plants and the insects has some bearing on the problem of feeding habits. The Umbelliferae, of which there are from thirteen hundred to fifteen hundred species, grow for the most part in the boreal, boreal-subtropical and austral floral regions of the earth. The four areas richest in Umbelliferae are the oriental region, middle North America, southwestern South America and Australia. Rutaceae, on the other hand, are even more wide-spread, growing in tropical Africa, Asia and South America as well as in the temperate regions. *Aristolochia* is more wide-spread in the hot and warmer parts of the world. The genus reaches its greatest development in South America and is almost lacking in Australia.

The *Aristolochia-Papilios* reach their greatest development in the tropics, Africa excepted. In North America there are but two species. Of the fifteen species of *Papilio* in Australia but two are *Aristolochia*-feeders. The group is absent from Europe and Africa. Feeders on Rutaceae are much more cosmopolitan than other species

of Papilio. Finally, there is the restricted occurrence of Umbelliferae-feeders. *P. hospiton* and *P. alexanor* are confined to the regions around Sardinia. Their close relative, *P. machaon*, is distributed throughout the temperate regions of the Old World. A race of *P. machaon* is found in Alaska. *P. ajax*, also closely related, occurs throughout eastern temperate North America and along the mountains of Central and South America to Chile. In western America are found *P. bairdi* and *P. zelicaon*. In Australia the most closely related species to *P. machaon* is *P. demoleus* which with *P. ophidecephalus* and *P. constantinus* also occurs in parts of India. It is seen that *P. machaon* bridges the gap between the New and the Old Worlds. All other Umbelliferae-feeders are closely related to it with the exception of *P. paeon* Boisd., which is in the *Thoas*-Group. In departing from the feeding habits of the genus, the Machaon-Group has adopted a family of plants characteristic of temperate regions. Undoubtedly the group occupies its present range because of the presence of Umbelliferae in those areas.

These ideas on the evolution of the feeding habits of the Papilios are naturally provisional at the present time due to the large extent of the field that is now only in the process of exploration. They are presented to show that further investigation along these lines should lead to valuable discoveries concerning the problems of feeding habits.

It is a pleasure to extend thanks to Dr. Austin H. Clark and Dr. D. H. Linder for their generous coöperation and numerous courtesies.

SUMMARY

A series of complex chemical compounds present in the essential oils of Umbelliferae impart characteristic odors to the plants of this family. Species of Papilio which feed on Umbelliferae are attracted by these chemicals. Although the attractant chemicals are most common in Umbelliferae, they occur sporadically in other families. Papilios now feeding on umbelliferous plants originally fed upon Rutaceae. The transition from one plant family

to the other took place because of the presence of identical attractant chemicals in both families. The present distribution of the genus *Papilio* is related in part to the distribution of the host plants.

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REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of the *AMERICAN NATURALIST*, in that they deal with the factors of organic evolution. No attempt is made to secure a complete coverage of the pertinent literature, or a uniform treatment. For contributions of major interest, however, interpretive reviews rather than abstracts are favored. During the first year there will be included reviews and notices of selected items which appeared in 1939 and 1940, as well as currently in 1941.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants.

By JENS CLAUSEN, DAVID D. KECK and WILLIAM M. HIESEY.
Carnegie Inst. Wash. Publ. 520, 1940: i-vii, 1-452, figs. 1-155.
\$3.50 (paper), \$4.50 (cloth), postpaid.

BIOLOGISTS who have known of the extensive transplantation experiments supported by the Carnegie Institution since 1922 have long awaited the publication of this sequel to Darwin's "Origin of Species." Many will feel that it will rank among the outstanding publications of the century on the theory of evolution. It is therefore gratifying, and perhaps significant, that, unlike a number of more or less major contributions of recent years, this one does not start with statements comparing Darwin's and the authors' views, in such a way as either to discredit the greatest biologist of all time or to levitate the new authors to a like height.

The presentation is straightforward and essentially scientific; moderately technical though sufficiently clear for biologists of all branches. Factual material predominates. The prodigious quantity of new experimental data is well summarized and generously illustrated by figures, graphs and tables. A total of 368 pages is devoted to unpadded accounts of the transplantation experiments with *Potentilla*, *Horkelia*, *Zauschneria*, *Penstemon*, *Achillia*, *Artemisia* and miscellaneous other genera of western plants. An interpretive attitude is maintained through-

out, but general and theoretical discussions are largely restricted to a few introductory pages and to the concluding chapter of 22 pages. Balance and strength of treatment were attained by the intimate association and fine teamwork of cytogeneticist Clausen, taxonomist Keck and plant-breeder Hiesey. In fact, one of the most significant contributions of these coworkers has been their part in breaking down the long-too-high barriers between the several disciplines of biology.

On introductory pages there are given briefly the background and history of the Carnegie experiments into the nature of species. Especial tribute is paid Dr. Harvey Monroe Hall, who initiated the present work. A "Glossary of Important Terms" tells at the outset that the authors are following Turesson's concepts of *cenospecies*, *ecospecies* and *ecotype*. "Purpose and Principles" are succinctly stated. "The object of the varied-environment experiments has been to discover principles that govern the distribution of plants and their organization into natural units." There is briefly recounted the gradual shift of the project from extensive and natural transplantations between many scattered stations on an altitudinal transect, to the concentration of the experiments at three cultivated gardens, located near the coast of California at (1) Stanford University (for some years the general headquarters for these researches), and in the Sierras at (2) Mather (1,400 meters) and at (3) Timberline. At Mather moist-sunny, dry-sunny, dry-shady and moist-shady plots were maintained, and at Timberline a dry-slope substation supplemented the main meadow garden. These stations are given general and climatological descriptions (it is difficult to understand why original data on the local climates of the actual sites were not used, in place of Weather Bureau data for more or less similar locations—in an area where the climatic pattern is a very fine mosaic). Increased concentration of the operations and standardization of methods with the years is indicated. Reciprocal transplants between many natural habitats, which were earlier practiced by Clements and Hall, and which utilized plants with different modes of reproduction, were gradually and almost wholly re-

placed by simple clone transplants, so that genetically identical stocks might be maintained, and grown in the gardens of the three stations, under conditions which permitted constant observation and the keeping of trustworthy records.

In this concentration and standardization of methods lie both the strength and the weakness of these experiments. The growing of clone members in a few demonstrably uniform gardens allowed the accumulation of data in adequate quantity and sufficiently comparable for statistical analysis, insured the reliability of the lineage records, and avoided the chance of the confusion of results through the action of selection and mutation in successive generations of transplants. Even so the experiments remain replete with variables that are difficult or impossible to measure. One wonders whether it would not have been desirable to have carried the elimination of extrinsic factors to the minimum, by growing all plants at one central station, in chambers wherein all climatic, edaphic and biotic factors would be rigidly uniformalized and altered at will.

The main weakness of the research, if such there be, lies as stated in the rigid simplification of the technique; and perhaps also in what seems to be the fixed conviction of the authors that environmental modifications are not closely related to speciation. The parallelisms between direct and genetic effects seem almost grudgingly admitted (at least are not prominently tabulated or statistically compared), though to many investigators of speciation, Neodarwinians included, the observed similarity between environmental and genetic adaptations is a most striking phenomenon—and a central problem. Perhaps the authors were reacting against the classical yet unreliable experiments of Bonnier and the reputedly similar researches of Clements—both of whom claimed to have proved that low-elevation plants when transplanted to high elevations become transformed within a few generations to the corresponding alpine species or races. We can imagine followers of Bonnier and Clements imputing the charge that Clausen, Keck and Hiesey not only allowed their convictions to direct their observations and to color

their presentation, but also that they so restricted their experimental program as to lessen the chance that transformations would be effected. Did not the authors too hastily and uncritically dispose of the results of Bonnier and especially those of Clements? In more varied environments, or under sexual reproduction, might not the modifications of lowland types at high altitudes have more nearly paralleled or even duplicated the genetically fixed characters of alpine forms? Are not organisms genetically so constituted that they may rapidly adapt their inherited characters to fit new environments? (The reviewer's observations on the fish populations of isolated desert water leads him to think of speciation as a process much more rapid than commonly thought.) Are there not some still imperfectly appreciated and intimate relations between genes and environment? Let the reviewer hasten to add that he interprets the great mass of available evidence as favoring most of the interpretations of Clausen, Keck and Hiesey. The problem, however, can hardly be regarded as finally settled. The views of Bonnier and Clements and even of avowed Neolamarckians and extreme sceptics of adaptation, all call for thorough, objective tests. The authors of "Experimental Studies on the Nature Species" were in a position to have made and presented many such tests—more directly, more fully and more statistically than they did.

Some fundamental adaptational relations are treated with mere statements, though clinching statistical tests could readily have been provided from the mass of new data, and would have been extremely welcome, in view of the hypercritical attitude of many biologists toward adaptation and selection. Entirely too many relations are illustrated by examples rather than by statistical treatment. Surely from these extended experiments one might have expected that each vital point would be subjected to objective test. Repeatedly the transplants of coastal or mid-altitude ecotypes at Timberline, though demonstrably changed in height, vigor and time of flowering (characters by the way that seem to have been regarded as of systematic importance), are claimed to have retained all the proper diagnostic features, yet readers

are forced to take this important statement largely on faith. At times the characters that fail to change are enumerated, or specified features are held to be "unfailingly replicated," but without presentation of factual data or clear illustrations. Progressive changes in the altered environment are emphatically denied (though the gradual weakening of stocks in successive years is often mentioned), and immediate recovery on return transplantation is avowed,—usually without any detailed evidence and never with adequate statistical data. Few modifications other than height of plant, number of stems and earliness of flowering are analyzed, yet many other changes were induced, some of which, like increased anthocyanin pigment, parallel systematic differences. For at least one ecospecies, the full range of modifications should have been objectively demonstrated. Perhaps more intensive work on single ecotypes would be desirable to amass data of overwhelming significance on critical points.

Despite its length and its extensive coverage of many topics from varied points of view, this book will be scanned in vain by many evolutionists for discussions of aspects of speciation in which they are particularly interested. Ecotypes are clearly demonstrated and well treated, but clines (graded ecotypes) are scantily considered (though indicated by such data as that on plant heights shown in Fig. 21). "Saturation effects" are disregarded. The tendency of adaptations to force an organism to develop and live in harmonious adjustment with the usual conditions of existence in its local environment is indicated here and there but not adequately generalized upon. Races are regarded without query as incipient species. Intergradation between subspecies is not analyzed in detail. Parallels with zoological evidence would have enriched the philosophical discussions, but were entirely unmentioned save for one reference to Dobzhansky's work on differentiation in *Drosophila*. It is to be hoped that the authors will bring their data more fully to bear on the many problems of adaptation and speciation.

The outstanding greatness of this monograph has led the reviewer to point out what seem to him to be de-

ficiencies, perhaps because he sought for more than he could possibly have hoped to find in any one book on speciation. It is indeed a monumental work, a strong candidate for the classics on evolution. It is also a major contribution to systematics, to ecology and to genetics. It sheds more light on the problems of speciation than any group of recent contributions. Species are dissected into their elements, and the elaborate adjustment of ecotypes to their environments is portrayed with unusual completeness and clarity. Speciating populations are made to live like organisms before our eyes. A potential species is dramatically produced in the cytogenetic research on *Zauschneria*. As seldom before, different disciplines of biology have been brought into one cooperative enterprise, to the mutual advantage of these specialties and to the further solution of the central problem of all biologists—the origin of species.

Why Men Behave Like Apes and Vice Versa or Body and Behavior. By EARNEST ALBERT HOOTON. Princeton: Princeton University Press, 1940: i-xxv, 1-234, 23 pls. (unnumbered, though referred to by number in text). \$3.00.

WHY Men Behave Like Apes and Vice Versa" has undeniable reader appeal, but describes this new Hootonian effusion much less adequately than does the generally-to-be-unquoted subtitle, "Body and Behavior."

The beginning of this book is its most auspicious part, for in the introductory "Harangue on Human Affairs" Hooton lays out, in his best journalistic style, a biological philosophy of man that has seldom been excelled in lucidity, daring and force. Although the author states that he prepared this introduction largely to relieve reviewers of the need to read further, this reviewer continued to the end, occasionally wondering why, or wishing he hadn't, but on the whole in happy appreciation of Hooton's wisdom and wit. The five sections of the main text, amplified from Vanuxem Lectures delivered at Princeton, carry as their main thread the contention that the bodily makeup of man is primarily involved in his functions, behavior and culture—all the quasiscience of sociology to the contrary notwithstanding. Starting with infrahuman primates, and repeatedly comparing apes with men to the dis-

paragement of *Homo*, the author points out how closely the peculiarities in behavior vary with taxonomic position. Grasping at fragments of information, in the clear understanding that a trifle of fact is weightier than an immensity of unverified theory, he then tries to determine and tell whether extinct species of Hominidae had peculiar, inborn ways. Next treating living types, he presents data which is held to indicate that the principle of correlates between race and culture still holds true, though he admits the complexity and weakness of the evidence when entire primary races are considered. In nations and ethnic groups some historical consistency of behavior through changing conditions is held to lend meaning to the variations of culture with race, for certain racial types tend to dominate nations (the chief discussion of this point, though not bearing decisively on the main argument, concerns the racial constitution of the Irish as indicated by the author's year-long study). Largely on the basis of Hooton's extensive work on the physical structure and the ways of American criminals, the differentials of body and behavior are finally held to be correlated in the individual. Several of the efforts to classify individuals within a race by somatological peculiarities are treated, usually in ridicule, but Sheldon's recent analysis of human constitutional types is given much space and full illustration, and is accorded a praise that seems to have been generally reserved and accumulated.

It is difficult for a biologist to understand why any student should doubt that human races have behavioristic as well as structural differences, for that is the general rule in animal kinds and is such a common observation for *Homo sapiens*. Nevertheless, it is obvious that Hooton's rational views along this line are very widely combatted by sociologists (as might be expected) and even by fellow anthropologists.

As a genuine scientist, Hooton would probably not expect all his thoughts and research results to be accepted by all biologists (obviously he has little hope of making headway with the quasiscientists). The reviewer would take exception to Hooton's thesis that race and ancestry are

clearly indicated by the combination of a few diagnostic traits in individuals of the notoriously "heterozygotic races of mongrel hybrids" that constitute modern man. Much may be learned from the analysis of combined characters, but there is little in either comparative taxonomy or genetics to support Hooton's main contention. As the author admits, most nations tend to become new races, through general hybridization, inbreeding and selection. Instead of denoting long lineage, common phenotypic traits may represent the like results from the crossing of diverse pairs of parents, or may be due to various chance reassortments of genes, or even to new mutations, either identical with the old or different yet producing like effects. Intensive studies of intergrading subspecies in various species of animals give indications that similar types of individuals have been repeatedly produced, through parallel evolution or through diverse speciation processes.

Liberated from the net of mysticism with which man's mind has entangled itself, and allergic to the unscientific methods of most savants who profess to be students of man, yet activated withal by an intense social consciousness, the brilliant Hooton strives to build up a real biology of man. In the reviewer's mind there is no greater human need, for man can hardly hope to endure indefinitely except through conscious control of his evolution, physical as well as cultural. Would that there were enough torchbearers like Hooton, to really light the world!

O. C. Marsh. Pioneer in Paleontology. By CHARLES SCHUCHERT and CLARA MAE LEVENE. New Haven: Yale University Press, 1940: i-xxi, 1-541, frontisp., pls. 1-30, figs. 1-33. \$5.00.

THOUGH lacking the dramatic sweep of many modern biographies, this thoroughly prepared and excellently printed treatise on the life and accomplishments of Othniel Charles Marsh will have a wide appeal. It will prove of keen interest not only to vertebrate paleontologists but also to specialists in other geological and zoological fields, and particularly to the general biologist. Through their common focus of interest in organic evolution, scientists of many disciplines will be attracted to this story of a

prominent apostle of Darwinism, whose discoveries of toothed birds, of the equine lineage and of other phyletic lines were prominent factors in the acceptance of evolution by both scientist and layman. The huge dinosaurs, flying dragons and the amazing array of other extinct creatures found and reconstructed by Marsh fired the imagination of the general public as well as of scientific men throughout the world, and the retelling of these discoveries should have a similarly broad appeal. The thrilling story of the early quest for vertebrate fossils in the Wild West is a significant chapter in the westward movement, and provides an item of interest for all.

This well-documented biography is in itself an inductive treatise into the facts and circumstances which illustrate the life of one of the most colorful characters in American science. The senior author's capacities as an interpretive scientist, supplementing his intimate contacts with Marsh and his environment, have given the life story not only accuracy and fullness, but also appraisal, interpretation, and correlation with scientific progress during Marsh's time. The long connection of the authors as well as of Marsh with one of our great universities explains an attitude toward Yale that may appeal to some as chauvinistic.

The long, bitter struggle between Marsh and Cope could not of course have been neglected, but is rather apologetically recounted here and there throughout the book. The reader is wisely left with the impression that this notorious conflict, as well as Marsh's disagreements with other scientists, his own assistants and public officials, were futile events, pertinent to a passing age and now more properly the subject of regret than of amusement. What greater gain might have been attained, had the two masters continued through their careers in active and constructive cooperation!

Marsh is pictured as a forceful man of deep intellect, able to transform into great scientific accomplishment the subsidies so generously provided by a wealthy uncle. It is shown that he was driven by an intense and undying love for discovery, coupled with an insatiable instinct of collecting. Living as though he had never to die, Marsh

continuously undertook far more than even he with his mental and financial endowments could accomplish. He completed only three of many projected monographs (any one of which, however, would have assured him leadership in vertebrate paleontology). As shown by a full bibliography, Marsh did publish, from 1861 to 1899, about 300 papers and notes. This prodigious contribution was supplemented by several unfinished treatises and large unworked collections, which have served and continue to serve as the basis for outstanding monographs and shorter publications, largely by former assistants and colleagues. Marsh's total legacy to science is almost immeasurable.

Visual Outline of General Biology. By GEORGE CHILD. Students Outline Series. New York: Longmans, Green and Co., 1939: i-iv, 1-97. \$0.75.

In highly condensed outline form this paper-bound booklet provides for elementary students a surprisingly complete coverage of the fundamentals of General Properties of Living Things, Nutrition, Irritability, Reproduction, Heredity, Evolution and History of Biology—useful for review and as a syllabus for lectures.

The Theory and Practice of General Science. By H. S. SHELTON. London: Thomas Murby and Co. (New York: Nordemann Publ. Co.), 1939: i-vii, 9-123. \$1.05.

We have here a discussion of the advantages of teaching general science rather than specialized courses in secondary schools; of the difficulties T. H. Huxley, J. J. Thompson and others have had in trying to introduce general science into the curriculum of English schools; and of the content of such a course, how it should be taught so as to integrate the whole subject, and how teachers can be prepared for the task. The treatment is almost wholly from the standpoint of British pedagogy.

Fleas of Eastern United States. By IRVING FOX. Ames, Iowa: Iowa St. Coll. Press, 1940: i-vii, 1-191, pls. 1-31. \$3.00 post-paid.

Essentially a systematic treatment, this book gives synonymy, description, records and hosts for each species in the region. The five-page Introduction covers Collection and Preservation, Morphology and Terminology and

Life History and Control. Synonymic Index, Host Index and Selected Bibliography are included.

Variations and Relationships in the Snakes of the Genus *Pituophis*. By OLIVE GRIFFITH STULL. Bull. U. S. Nat. Mus., 175, 1940: i-vi, 1-225, figs. 1-84. 35 cents (Superintendent of Documents).

THIS well-documented treatise is one of those general systematic revisions that will be of interest to the increasing numbers of students of speciation. It follows closely the precedent established by Alexander G. Ruthven in his pioneering revision of the garter snakes (*Thamnophis*). The theoretical interpretations deal primarily with the origin of phyletic lines and the direction of their speciation, rather than with the principles of phylogeny. It is concluded, however, that in general the evolutionary lines, represented by present distribution, are marked by continuous modification in one direction. From the assumed center of origin the numbers of scales are held to decrease peripherally, in what is assumed to represent the speciation trend. It is further concluded (p. 12) that "the relative constancy of a character throughout the group is the best index to its diagnostic importance."

L. M. B. C. Memoirs on Typical British Marine Plants & Animals. XXXII. *SEPIA*. Univ. Press Liverpool, 1939: i-vii, 1-184, frontisp., pls. 1-24, figs. 1-4. 12/6.

ANOTHER of a long series issued by the Liverpool Marine Biology Committee, this memoir thoroughly monographs the anatomy of a type animal—the cephalopod, *Sepia*. Such treatises are fundamental not only in education but also in scientific advance, particularly in phylogeny.

Man and the Living World. By E. E. STANFORD. New York: The Macmillan Co., 1940: i-xxviii, 1-916, figs. 1-451. \$3.50.

WITHOUT venturing an appraisal of the pedagogical value of biological survey courses in general or of this book in particular, the reviewer expresses his conviction that Dr. Stanford has been eminently successful in his "attempt to develop a fairly comprehensive organization of principles and facts for text use in what are commonly called biological survey courses." The vast amount of

information concentrated in this attractive volume should render it also a valuable addition to public, school and home libraries. Any biologist would do well to go over the book, if for no other purpose than to be shown what a small niche he fills in his scientific environment. Legitimately there is included in this "biology" not only the conventional zoology and botany, but also the elements of such subjects as human anatomy and physiology, sex hygiene, foods, nutrition, disease and its treatment, bacteriology, anthropology, agriculture, animal husbandry and conservation. The almost uniformly well-balanced and reliable material has been very readably put together. Human interests are emphasized throughout, but hardly in such a way as to induce an anthropocentric attitude. There is presented the sound biological basis of healthy and progressive human life, racial as well as individual. Problems inevitably raised by such a treatment are neither ignored nor accorded one-sided statements, but are met squarely and impartially.

Life Histories of North American Cuckoos, Goatsuckers, Hummingbirds, and Their Allies. Orders Psittaciformes, Cuculiformes, Trogoniformes, Coraciiformes, Caprimulgiformes, and Micropodiiformes. By ARTHUR CLEVELAND BENT. Bull. U. S. Nat. Mus., 176, 1940: i-vi, 1-506, pls. 1-73. 75 cents (Superintendent of Documents).

ORNITHOLOGISTS look forward eagerly to each new volume of Bent's "Life Histories," and general biologists find in this treatise a wealth of base data, brought together from the general literature. This volume in one section reflects the views of the bird lover rather than the scientist, for the statements on the economic status of the kingfisher are uncritical, propaganda-like.

Australian Antarctic Expedition, 1911-14. Under the Leadership of Sir Douglas Mawson, D.Sc., F.R.S. Scientific Reports. Series A: Vol. 2, *Oceanography*, pt. 2, 1939, "Tidal Observations," by A. T. DOODSON (pp. 61-85, figs. 1-7, pls. 4-6, price 4s); pt. 3, 1939, "Soundings," by JOHN K. DAVIS (pp. 87-102, pls. 7-8, price 2s/6d); pt. 4, 1940, "Hydrological Observations," by DOUGLAS MAWSON (pp. 103-25, price 3s);

pt. 5, "Marine Biological Programme and Other Zoological and Botanical Activities," by DOUGLAS MAWSON (pp. 127-67, figs. 8-12, pls. 7-15, price 7s/6d). Series B: Vol. 5, "Meteorology," pts. 1-3 and appendix: 1-281, figs. 1-5, pls. 1-4, price 40s.

Illustrated Key to West North American Pelecypod Genera. By A. MYRA KEEN and DON L. FRIZZELL. Stanford University, California: Stanford Univ. Press, 1939: 1-28 (offset printing). \$0.75.

Biological Stains. A Handbook on the Nature and Uses of the Dyes Employed in the Biological Laboratory. By H. J. CONN. Geneva, N. Y.: Biotech Publications, 4th ed., 1940: 1-308. \$3.40.

LESS new material has been added to the fourth edition of this standard treatise than to the previous revisions, but the whole text has been subjected to a critical revision to correct errors. As before, the book is sponsored by the Commission on Biological Stains of the National Research Council.

French-English Science Dictionary for Students in Agricultural, Biological and Physical Sciences. New York and London: McGraw-Hill Book Co., 1940: i-viii, 1-546. \$3.50.

THIS dictionary, giving the main English equivalents for numerous French words, including scientific terms, follows the same author's German-English Science Dictionary. These books should prove particularly helpful to graduate students.

EVOLUTION NEWS

A Conference on Maintenance of Pure Genetic Strains, called by the chairman of the National Research Council, was held in Washington on January 27, 1940, and has been supplemented by correspondence and by a report prepared by a smaller committee. Discussions were centered about the needs for pure strains in biological and medical work, the methods now used in the culture and ready supply of stocks of various type organisms, and the developments required to insure the maintenance and supply of pure strains.

As one result of the Symposium on Speciation held a

year ago at the Columbus meeting of the American Association for the Advancement of Science, a movement has been underway for the organization of the group of biologists interested in the problem of speciation. Professor Alfred E. Emerson, of the University of Chicago, is taking the lead in this meritorious move, which was suggested by Julian Huxley, the visiting participant in the symposium (Huxley has been prominent in a similar movement in England). The consensus of opinion seems to be that another journal-issuing society is not desirable at present, but that some form of organization would serve the interests of the rather large and growing number of speciation workers and help to organize speciation as a definite and progressive field of biological endeavor. The following statement on the society in formation has been prepared by Professor Alfred E. Emerson:

THE SOCIETY FOR THE STUDY OF SPECIATION

Objects.—The need is felt by many students of speciation for a greater degree of integration between the various fields. Those contributing to an understanding of the factors influencing speciation are often in fields and institutions which have little direct contact with those who are attacking the problem from somewhat different angles and are using different techniques. Both workers and bibliographies are scattered. The general object of the society is to institute an informal information service which will tend to correlate the various approaches.

Fields of Interest.—The major field of interest is the dynamics of the origin of species. Obviously the analysis of the factors of speciation involves the study of divergence of populations classified as subgroups within the species. Therefore studies of the origin of local populations, races and subspecies are necessary parts of the study of speciation. Also many factors may be studied and verified through analysis of the evolution and stability of the higher taxonomic categories. There should be no limitation on the inclusion of any phase of evolution

that contributes to an understanding of the central problem of the origin of species.

The major factor complexes may be termed hereditary variation, isolation and selection. These may be subdivided into various types and mechanisms and numerous illustrative examples among plants and animals may be given. The recognized fields of Bacteriology, Botany, Zoology and Anthropology have long been interested in the general species problem. The biological sciences which obviously are making contributions to speciation and general evolution include Morphology, Cytology, Genetics, Biogeography, Ecology, Paleontology, Physical Anthropology, Comparative Psychology, Comparative Physiology, Embryology, Population Biology and Taxonomy.

Organization.—A group of scientists from various fields have joined an informal society called the Society for the Study of Speciation. This society has a secretary and an executive committee. The secretary is responsible for the general organization of the group and the publication of information for distribution. The various members will contribute this information. The publication program includes bibliographies, notes concerning original work, critical comments upon the work of others and news items of interest to the group. Any one interested in receiving the publications should join the society by sending his name and filling out the questionnaire. Any one wishing to contribute information for the booklets should send material to the secretary.

At the present time the following executive committee is functioning for the society: Edgar Anderson, John M. Beal, William Burrows, L. J. Cole, Lee R. Dice, Th. Dobzhansky, Alfred E. Emerson (*secretary*), A. C. Kinsey, W. M. Krogman, Karl P. Schmidt, George G. Simpson and Sewall Wright. When the permanence of the society is assured, a system of election by members will be instituted.

It is not desired that one more formal organization be

added to the large number of scientific societies already in existence, but the need is felt for an informal cooperative group of scientists willing to pass information from one to the other. Through anonymous donation, the initial expenses of organization have been provided for. It is contemplated that the society will become self-sufficient soon after it is organized, and the first information booklets have been mailed. However, the expenses should be kept to a minimum to cover the small costs involved in the issuing and mailing of the information booklets. It is suggested that the simplest and least expensive form of publication will best serve the needs of the members.

The original suggestion for organizing such a society in the United States came from Julian Huxley, who conferred with numerous individuals in this country. The need for such a society had been realized for some time and various local groups, as well as sections and committees of existing societies, had already been organized. It is hoped that this society can cooperate with these groups and extend its range to include scientists and organizations in various countries as conditions permit.

The secretary will attempt to help in coordinating the various fields and individuals. Many suggestions have already been received which deserve careful consideration and a cross section of opinion is included in the first booklet. A number of the suggestions, although laudable, involve more time than the secretary can devote to this undertaking or involve more of a financial structure than seems possible at the present time. Other suggestions are feasible but require more general expressions of opinion in order to be put into practice. The secretary, within the limits of his time, will attempt to bring the constructive suggestions before the society for consideration and democratic action.—ALFRED E. EMERSON, *University of Chicago, Chicago, Illinois.*

SHORTER ARTICLES AND DISCUSSION

THE HYBRIDIZATION OF WATER FERNS— *MARSILEA* AND *PILULARIA*

SEVERAL years ago we had occasion to carry out some experiments in the interspecific and intergeneric hybridization of water ferns. This was done in connection with a series of experimental studies of certain Marsileaceae, where some of the experiments of Leitgeb (1878) were repeated with modifications in which the experimental technique of LaMotte (1937) was employed. No difficulties were found in isolating some of the female gametophytes from the remaining portions of the mixed cultures coming from sporocarps before the appearance of sperms, in order to reintroduce them later and control the time of fertilization. The experimental material included *Marsilea quadrifolia* L., a species which has become naturalized in the eastern and central states, *M. crenata* Presl., a species native to the Philippine Islands and a species of *Pilularia* probably *P. americana* Nutt., whose sporocarps had been included in soil containing the spores of *Isoetes* collected by Dr. Chas. LaMotte near Marble Falls, Texas.

The two species of *Marsilea* are by no means closely related. *M. crenata* has crenate leaflets and much smaller sporocarps which are paired or sometimes solitary, while *M. quadrifolia* has leaflets with entire margins and has much larger sporocarps borne in pairs or occasionally in threes.

The megaspores of these three species were found to differ sufficiently in dimensions so that they could easily be distinguished from each other when grown together. These differences in size and shape therefore reliably identified the species to which the female gametophytes belonged, and the conditions were nearly perfect for some collateral experiments on hybridization between these species of water ferns.

Among the experimental results (Selett, 1935) which confirmed the general results of Leitgeb, it was found that the gametophytes of the three species do not develop at the same rate (room temperature about 85° F.), nor shed their sperms at the same time. In *M. crenata* the first sperms were observed 5 hours after placing the opened sporocarps in water; in *M. quadrifolia* 8–9 hours were required and in *Pilularia* 18 hours, for the appearance of the first sperms. The archegonia were matured in 15 hours in the two species of *Marsilea* and in 28–30 hours in *Pilularia*.

The knowledge of the difference in time required for the sexual maturity of the gametophytes made it possible to time the experiments on hybridization so as to introduce female gametophytes of known maturity into the cultures of the male gametophytes when sperms were actually present, and the presence and behavior of the sperms could also be ascertained by direct observation.

While these experiments on hybridization were conducted on a very small scale only, the results obtained were very definite, and may have value in pointing out some of the possibilities in this field of investigation.

The megaspores which remain attached to the female gametophytes are distinctive for each species, and it was possible to introduce the female gametophytes into the cultures containing the gametophytes of both sexes of the other species, and observe the reactions of the sperms as they inseminated the eggs of their own species and also those of the intruded foreign species.

In the cross *M. crenata* \times *M. quadrifolia* from 15 female gametophytes of the former introduced into the cultures of the latter, 2 were removed for special observation on a slide, and were eventually destroyed, while the remaining 13 were recorded and accounted for after the experiment. Among these, the eggs of 5 gametophytes appeared to remain unfertilized while 8 developed hybrid sporophytes. In the reciprocal cross (*M. quadrifolia* \times *M. crenata*), 8 out of 10 attempts were accounted for and recorded; of these, 3 remained unfertilized and 5 developed hybrid embryo sporophytes. In each case there were female gametophytes of the same species left with the male gametophytes. These served as controls indicating normal conditions in the male cultures and developed normal sporophytes which could have been kept growing indefinitely. All the 13 hybrid sporophytes appeared to develop normally until the first leaf reached a length of 8 mm, where they remained stunted but were kept alive for nearly 3 weeks, after which they all turned brown and died. No differences were noted in the hybrid sporelings coming from the reciprocal crosses.

Attempts were also made in hybridizing both species of *Marsilea* with *Pilularia americana* in reciprocal crosses. None of these intergeneric combinations was successful.

In the attempted cross *M. crenata* \times *Pilularia*, involving 14 female gametophytes of the former introduced into the cultures of the latter, all the eggs of these gametophytes remained un-

fertilized. In the reciprocal cross only one out of 6 attempts was accounted for, and this did not develop an embryo. In the attempts to make the cross *M. quadrifolia* \times *Pilularia*, using 8 gametophytes of the former, all eggs remained unfertilized. Likewise in the reciprocal cross, employing 6 gametophytes, no embryos were obtained.

A more detailed examination of some of this material under the microscope showed that the sperms of *M. quadrifolia* were attracted to the gelatinous material surrounding the megaspore and gametophyte of *Pilularia*, but the sperms from *Pilularia* did not seem to be attracted by the female gametophyte of *M. quadrifolia*.

The general results of these experiments indicate that it may not be possible to obtain intergeneric hybrids among the Marsileaceae; that interspecific hybrids between the two species of *Marsilea* may be obtained, but they grow and develop for several weeks only, and die while they are still in early sporeling stages.

These experiments are interesting to the geneticist when considered from the standpoint of the causes of interspecific sterility. The hybrid embryo sporelings are not only formed but they emerge fully and pass well into the stage of being green independent organisms, so that the arrest in their further development appears to be due to their genetic constitution. On the other hand, in seed plants the failure of an attempted hybrid cross may be similarly genetic; it may be due to difficulties in pollen-tube growth or to failure in fusion of nuclei in one or the other of two distinct fertilizations, resulting in a lack of development of both embryo and endosperm—in fact, there are numerous interdependent processes all contained within an ovule. This ovule may abort entirely without yielding sufficient information as to whether the basic cause of the sterility between species is genetic or more indirectly involved in some way in this very complex process of reproduction.

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SOME CRITERIA FOR JUDGING THE DEGREE OF POLYPLOIDY OF CELLS IN THE RESTING STAGE

THE determination of the presence or absence of polyploidy or of the degree of polyploidy in resting cells is frequently desirable. Various substitutes for the direct method, the counting of chromosomes, have been used. Meurman (1933) states that in the root tip of *Acer platanoides*, in spite of variations due to position and individual differences, the disparity in size of diploid and tetraploid cells is sufficient to permit their classification independently of chromosome counts. In the case of *Spinacia* this statement must be qualified. In many instances cell size is a good indication of the existence of polyploidy but a less reliable manifestation of its degree. In other cases no trustworthy estimate can be made on the basis of size. Sections of root tips, longitudinal or transverse, conceal one dimension of the cell. Size differences correlated with position are not always constant and the same may be said of the degree of vacuolization. In a region of great meristematic activity the size of a resting cell differs with the proximity of the preceding or succeeding mitosis.

In some more uniform tissues, where individual variations are small and mitotic activity is absent, cell size becomes a much more reliable guide. Blakeslee has found that the size of mature pollen grains is a valid index of polyploidy.

Nuclear size is, in general, a better criterion than cell size. It is free of variations due to vacuolization and largely independent of those associated with position.

Geitler (1937) has shown that in the polyploid larval tissues of some insects the X-chromosomes are distinct and heterochromatic, *i.e.*, they remain condensed and pycnotic in the resting nucleus, while all the other chromosomes behave normally. It is possible in these cells to determine the degree of polyploidy directly by counting the number of condensed X-chromosomes. This valuable method is apparently limited to a small group of insects.

De Mol (1927) pointed out that diploid and triploid *Hyacinthus* differed constantly in having two or three nucleoli respectively in their resting nuclei. The number and size of nucleoli constitute a better criterion of polyploidy than cell or nuclear size, at least in species with a small maximum number of nucleoli, since it is independent of variations due to cell size, position, vacuolization and all other tissue differentiations. By maximum number of nucleoli is meant the number seen in telophase before the fusion of nucleoli. In the root tip of *Spinacia*, where tetraploid and octoploid cells occur normally, this correspondence of number and size of nucleoli with degree of polyploidy is beautifully illustrated. The variety of appearances seen in telophase of octoploid divisions, where eight single nucleoli are in the process of random fusion, probably accounts for the opinion of earlier investigators that polyploidy arises by a process of nuclear fusion.

In the course of a study of the origin of the different grades of polyploidy in *Spinacia*, a new criterion of the degree of polyploidy of resting nuclei has come to light. When clearly discernible it is more reliable than the above-mentioned criteria and, when considered together with them, renders the interpretation of the degree of polyploidy of a resting nucleus very convincing. It is the number of heteropycnotic satellites present, either in direct contact with the nucleolus or joined to it by a thin thread.

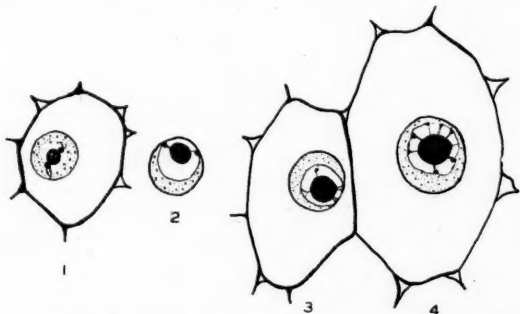


FIG. 1. Diploid cell from the calyptra with two satellites in contact with the nucleolus. Double chromonemata run from the satellites to the nuclear surface. FIG. 2. Nucleus ($2n$) from the youngest region of the periblem, the satellites are at a short distance from the nucleolus and joined to it by thin threads. FIG. 3. Tetraploid cell from periblem. FIG. 4. Octoploid cell from the same region of the periblem. All cells from the same root tip of a germinating *spinacia* seed. All figures $\times 900$.

Spinacia has a haploid number of six chromosomes. One of the six has a small satellite which, as is known in other cases, is heteropycnotic in the resting nucleus. A diploid cell in this species (Fig. 1) contains two small nucleoli in early telophase. In the resting stage these usually fuse to form one large nucleolus. Prophases almost without exception contain one large nucleolus. The cells of the calyptra are diploid. They are all in the resting stage in young germinating roots, and most of them have been in this condition since the end of embryo formation. The nuclei of these cells have a single large nucleolus with two small chromatic bodies, the satellites, in contact with it. From each of the satellites a single or double chromatic thread stretches across the clear region surrounding the nucleolus and joins the chromatic "reticulum" lying near the surface of the nucleus. In regions of mitotic activity the satellites are frequently not in immediate contact with the nucleolus but lie near the edge of the clear region (Fig. 2) and are connected with the nucleolus by single or double strands, the secondary constrictions of the SAT-chromosomes.

In the zone of the root where tetraploid cells occur the resting nuclei of these larger cells show four satellites (Fig. 3) connected to one large nucleolus or distributed evenly among from two to four smaller nucleoli. In the octoploid region of the root eight satellites can, in clear cases, be found showing similar relations to one very large nucleolus (Fig. 4) or to a varying number of smaller ones.

Since, as in *Spinacia*, a heteropycnotic satellite has the same appearance in the resting stage and at metaphase, and since it is situated in the clear region surrounding the nucleolus where it can readily be observed, counting the number of satellites should, in favorable cases, yield as certain information regarding ploidy as is obtained by counting chromosomes at metaphase.

In species with more than one pair of satellited chromosomes this method will probably be more difficult and impracticable. It has proved to be of value in a study of the much-disputed question of the origin of polysomatic cells of developing root tips.

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OBSERVATIONS ON THE GERMINATION OF *ARAUCARIA BIDWILLII*

Araucaria Bidwillii Hook, the Bunya-Bunya tree of Australia, is grown in California parks and sometimes on large lawns. It is a large picturesque tree and has large cones that often approach the size of a man's head. In August, 1939, cones were received and several of the large seeds were planted. The seed germinated readily, but no true leaves appeared even after several months.

The cotyledons are surrounded by a large source of food which apparently can nourish the young plant for months while its root system is becoming established. The seed upon germination develops an enlarged fusiform radicle from which the true leaves are later grown. The seed and the fusiform radicle show an intermediate plant tissue which soon decays away, leaving the remains of the old seed separated from the newly established plant.

Three germinated seeds were accidentally broken off from the fusiform radicle when being examined, but this did not affect the young plants adversely, since they all grew and developed true leaves and that much sooner than three other seedlings with the seeds attached. These seedlings with the seeds attached developed a root system, but the seed shells were still in place one year after planting, were empty and probably had been for some time. Within the seed shells that were still in place, plant growth of 1 to 2 inches had taken place. This growth had rudimentary leaves, while the three plants from which the seed were broken off were well branched, leafy and about 8 inches in height.

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